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THE CRAWFISHES OF THE STATE OF PENNSYLVANIA.

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I. INTRODUCTION.

The present Memoir is a continuation of, and an enlargement upon, the preliminary paper published some time ago in the Annals of the Carnegie Museum (Vol. III, 1905, p. 387 *et seq.*) under the title "The Crawfishes of Western Pennsylvania." The object of these publications is to furnish the student with an account of the crawfish-fauna of the state of Pennsylvania as complete as possible, not only from the morphological and zoögeographical, but also from the biological, ecological, and economic standpoint. It is now believed that it is possible to present an approximately complete report upon this important branch of the fresh-water fauna of the state, and in the prosecution of the studies of the author a number of questions were raised, the solution of which proved to be highly interesting.

It may be well at the beginning to give an outline of the work done. At the outset the writer resolved to go over the whole state, and to collect specimens in as many different localities as possible. Very soon, however, it was discovered that the different parts of the state are of unequal interest. Large tracts, located chiefly in the central, northern, and northeastern parts of the state, proved to be rather uninteresting, only one species of crawfish being present in them, while the western, and chiefly the southwestern, and again the southeastern sections offered more variety. Thus it became necessary to pay more attention to the latter areas. The uninteresting regions were entered only in a few cases, but a good deal of work was done around their edges, in order to trace their limits as accurately as possible.

The location of the writer in Pittsburgh was advantageous, being central within that section of the state which offered the greatest number of problems. Most of

the collecting excursions were undertaken with Pittsburgh as a base. However, on three occasions the base was shifted. Visits were twice made to the eastern part of the state, where the writer spent several weeks in September of the years 1904 and 1905 in Philadelphia and its environs, and once to the eastern central part, where several days were spent in Harrisburg in June, 1905. The latter visit was marred by rainy weather.

The work of collecting was done for the Carnegie Museum by the writer in connection with his duties as Curator of Invertebrate Zoölogy, and all the necessary expenses were paid by the Museum. In order to give an idea of the amount of field-work done, a few statistics may be interesting.

Altogether one hundred and thirty-eight days were spent in the field, counting only those days on which actual collecting was done: four days in 1903; sixty in 1904; and seventy-four in 1905. A few additional records were obtained in 1906.

The distances covered in travelling were as follows :

Bv	rail.	in 1904	3238	miles.	Total.	
ũ	44	" 1905	7579	"	10,817 miles.	
Ву	team	, in 1904	12	miles.		
"	**	* 1905	26	"	38 miles.	
On	foot,	in 1903	3 :	miles.		
"	"	" 1904	173	66		
"	"	" 1905	209	"	385 miles.	
	Gra	nd Total			11,240 miles.	

Collections were made at about one hundred and fifty-six different localities, most of them in the state of Pennsylvania. Of the sixty-seven counties of the state thirty-nine were visited.¹ Besides, visits were made to a number of localities situated in neighboring states, namely : in Camden County, New Jersey ; in Allegheny and Garrett Counties, Maryland ; in Morgan, Mineral, Tucker, Preston, Monongalia, Pleasants, Wetzel, Marshall, Ohio, Brooke, and Hancock Counties, West Virginia ; and in Harrison, Carroll, and Stark Counties, Ohio.

The material secured on these excursions belongs to and has been deposited in the collections of the Carnegie Museum, and comprises 303 entries in the Catalog, including 1869 specimens. But this does not represent the entire number of specimens collected, since large sets, which have not been cataloged, have been set aside as material for exchange, study, etc.

¹Material was secured, seen, or was previously known from fifteen additional counties, so that only thirteen are not explored, namely : Carbon, Juniata, Lackawanna, Lebanon, Mifflin, Monroe, Montour, Pike, Schuylkill, Snyder, Snsquehanna, Union, and Wyoming. All these belong to the central and northeastern section of the state, where only one species of Cambarus (*C. bartoni*) is to be expected, with the exception of those localities which are in the immediate vicinity of the main branches of the Susquehanna River, where also *C. limosus* may be present (Juniata, Montour, Snyder, and Union Connties).

Practical experience gradually revealed to the writer the best method of collecting crawfishes. At first the writer was rather inexperienced, and did not know where to look for certain species. But the necessary knowledge and skill were soon acquired.

To collect the species living in streams, rivers, and ponds requires no special effort; it is only necessary to wade into the water-course to be investigated, or to walk along its edge, and to discover the hiding-places of the crawfishes, which is done by turning over stones. A pair of rubber-boots, or wading-stockings, protected by ordinary bathing-shoes, is very convenient; and also a small landing-net, the bag made of minnow-netting. Frequently specimens may be caught with the hand. In certain places, and in the case of certain species (*Cambarus limosus*) waterweeds often furnish hiding-places, and here it is advisable to use a larger landing-net with a long handle, which is pulled or pushed through the weeds.

More work is required in collecting the burrowing species. The first thing is to locate them, which is generally done by searching for the mud-chimneys built over their burrows. But it is not always easy to find these, particularly in late summer and autumn, the chimneys being then rather inconspicuous. I generally first ascertain favorable localities, such as swampy places in the bottom-lands, and springy places on the hillsides. It is a very good plan to closely watch ditches by the roadsides. Here the chimneys generally are easily detected, and in the neighborhood of such places large colonies often may be found. After a burrowing form has been located, the most difficult work begins, for the inhabitant of the burrow must be dug out of its hiding-place. Care must be taken while digging not to injure the crawfish. Sometimes the work can be done with the bare hand, but only in those rare instances in which the burrows are in very soft ground. Generally the work must be done with pick and shovel, but, as it is inconvenient to carry these cumbersome tools along on an excursion and a gardener's trowel is a little too weak, I have found a pioneer's bayonet, such as is used in the United States Army, to be a tool which beautifully serves the purpose. These bayonets may be had in gunand ammunition-stores in the larger cities, and are practically indestructible.

After locating a crawfish-hole, I begin to dig down around it, loosening the dirt with the bayonet, and removing it with my. hands, always taking care not to lose trace of the hole. Generally it is necessary to go down upon the knees (rubber boots are useful here), and even the belly, in order to reach the bottom of the hole, to which the crawfish usually retreats when disturbed. Often, however, it retires to a side branch, in which case it is not necessary to dig so deep. As soon as it is felt beginning to pinch with its claws, it is a sure sign that the crawfish has been

cornered, and cannot retreat further. It is then readily secured, but care must be taken not to pull it out by the claws, which may be easily broken off, thus damaging the specimen. The creature should be always seized by the carapace.

Sometimes this work is very difficult and tedious, and I have often been compelled, chiefly in the case of Cambarus carolinus, to dig as deep as three feet before succeeding in capturing the crawfish. In order to avoid unnecessary labor as far as possible, I select burrows in which the water stands near the surface, refusing those which evidently go for a long distance through dry soil. Generally there is ample opportunity to choose between the numerous burrows of one and the same colony of chimney-builders. Now and then it happens that the work is rendered easier by the action of the crawfish itself. It occasionally comes to pass that, after having disturbed the entrance of the hole by digging down far enough to reach the water, the crawfish may be seen coming forward, apparently trying to ascertain the the cause of the disturbance. This is a good chance to seize it, but one must be quick, since it generally is the only chance to get it easily, although I remember cases when the crawfish came out again and again, just so far as to be plainly seen, but darted back at every attempt to seize it. Males are more frequently caught in this way than females, and such captures are made most frequently in cloudy or rainy weather. It is very rarely that there is a chance to capture the crawfish at the mouth of the undisturbed hole, when it is sitting at or near the top of the chimney, or on the ground away from the hole. This happened only once or twice in my experience.

I have tried to discover means of compelling the crawfish to come out of its burrow, but without much success. Bisulfide of carbon will not avail since it floats upon water. I tried chloroform, which sinks in water, but without success. Only once had I the satisfaction of driving a specimen of *Cambarus monongalensis* out of its hole by using unslacked lime. In this case I had dug a hole nearly three feet deep without being able to reach the bottom. I happened to have with me, especially for this purpose, a small tin box with unslacked lime, and dropped the contents into the hole, where it apparently sank to the bottom. Within three or four minutes the crawfish was discovered hurriedly working its way upward in the hole, and was easily taken. This method, however, can be used only in a limited way, since the holes generally are not straight enough to afford a chance to drop the lime to the bottom, and, if the lime becomes lodged somewhere above the point where the crawfish is staying, it drives it away from the mouth of the hole, and eventually kills it before it can be reached. (As to the use of lime for destroying crawfishes, see *infra*, VI, 4.)

The tools and the outfit needed for collecting crawfishes consist of rubber-boots (for work in swamps), or wading-stockings with low shoes (for work in streams), bayonet (for digging up burrowing species), and a landing-net with minnow-netting. These are indispensable. Further, a number of collecting jars are needed, with 75 per cent. to 80 per cent. alcohol, and I prefer to carry them in an ordinary fishing-basket, but any other portable receptacle will do. I do not recommend the use of formaldehyde, since it makes the specimens too brittle. In order to take specimens home alive, a so-called "bait-box" is most convenient.

I have no experience in baiting crawfish, and never attempted it, since the methods described above proved satisfactory. Furthermore, I have never (in Pennsylvania) used the seine, and I do not think that this would be necessary or advisable in this part of the country, although it may be tried to advantage elsewhere.

Besides the material secured by me in the manner above related, I made use of the older material preserved in the Carnegie Museum, which was collected by the following gentlemen : D. A. Atkinson, G. H. Clapp, E. Frost, B. Graf, J. L. Graf, E. Hays, S. N. Rhoads, A. T. Shafer, Q. T. Shafer, H. H. Smith, R. Taylor, W. E. C. Todd, M. A. Wertheimer, and E. B. Williamson.

I was aided in my researches by material kindly collected by various persons for the Museum, while my work was in progress, and to all of them I wish to here express my best thanks. They are the following members of the Museum staff: Mrs. Elizabeth Courtney, Mr. C. V. Hartman, Mr. D. C. Hughes, Mr. O. E. Jennings, and Mrs. O. E. Jennings.

The following gentlemen living in or near Pittsburgh furnished material: Dr. D. A. Atkinson, Dr. O. T. Cruikshank, Mr. R. Dornberger, Mr. D. Friel, Mr. F. E. Kelly, Dr. A. Koenig, Mr. A. Settlemoyer, and Mr. R. Settlemoyer.

Material from other parts of Pennsylvania was received from Professor A. E. Davison, Lafayette College, Easton, and Mr. H. Gera, Manayunk.

Specimens of our Pennsylvanian species were received from localities outside of the State from the following sources: Academy of Natural Sciences, Philadelphia, (material from Delaware, Maryland, and North Carolina. in exchange); Mr. H. Gera, Manayunk, (material from New Jersey); the late Mr. J. B. Hatcher, Pittsburgh, (material from Iowa); Mr. O. E. Jennings, Pittsburgh, (material from Ohio); Mr. S. Prentice, Pittsburgh (material from Kansas); Dr. R. Ruedemann, Albany, New York, (material from New York); Mr. F. Silvester, Princeton, New Jersey, (material from Maryland); Mr. E. B. Williamson, Bluffton, Indiana, (material from Kentucky, Indiana, and Michigan).

Very considerable help was received from the Department of Agriculture in Harrisburg. The State Zoölogist, Professor H. A. Surface, not only sent to me for inspection all the crawfishes in the collection under his charge, but also submitted to me material collected during the summer of 1905 by Mr. W. R. McConnell, who was in charge of a survey conducted by the State Zoölogist in coöperation with the Commissioner of Fisheries, Mr. W. E. Meehan. To Mr. Meehan and Professor Surface I am under special obligation for giving instructions to Mr. McConnell regarding the collecting of crawfishes, and to the latter gentleman for carrying these out in the most thorough way in parts of the state not visited by myself.

Finally, I was granted the privilege of examining the collections of the Academy of Natural Sciences in Philadelphia, where I found, aside from older specimens already used by Hagen and Faxon, valuable additional material, collected by Messrs. H. A. Pilsbry, E. G. Vanatta, H. W. Fowler, and B. W. Griffiths. I also received specimens for examination from Oberlin College, through the late Professor A. A. Wright and Mr. R. L. Baird; from the New York State Museum through Mr. F. C. Paulmier; and from Dr. P. R. Uhler in Baltimore, and Professor T. D. A. Cockerell, in Boulder, Colorado.

Last, but not least, my thanks are due to the Director of the Carnegie Museum, Dr. W. J. Holland, who not only granted the means for carrying on my work successfully, but has devoted much time to the editorial revision of the manuscript, and helped me in the preparation of the colored plates accompanying this memoir, which were made under his direction.

II. HISTORICAL REVIEW OF OUR SYSTEMATIC KNOWLEDGE OF THE CRAWFISHES OF PENNSYLVANIA.

The first species of the genus *Cambarus* ever described very likely came from our state. *Astacus bartoni* of Fabricius (1798, p. 407) was sent to its author by Professor B. Smith Barton, who lived in Philadelphia, (see Faxon, 1885*a*, p. 65) and presumably was collected in the neighborhood of that city.

The next record of a Pennsylvanian crawfish is given by Rafinesque (Nov., 1817), Astacus limosus, from the muddy banks of the Delawarc near Philadelphia. Another species mentioned by Rafinesque from this state, Astacus fossor, is not recognizable. Astacus limosus from the Delaware River was described a month later (Dec., 1817) by Say under the name of Astacus affinis.

Harlan (1835) mentions A. bartoni from the vicinity of Philadelphia, and this record makes Philadelphia the type-locality of this species.

Girard (1852) gives the following new localities in Pennsylvania: Cambarus

affinis = limosus, Schuylkill River at Reading, Bucks County; C. bartoni, Foxburg, Clarion County; Carlisle, Cumberland County; Berwick, Columbia County.

In Hagen's Monograph (1870) no new species are added, although he doubtfully records (p. 100) *C. obscurus* from the state, but this was done under the erroneous assumption that *Astacus fossor* of Rafinesque is the same as *C. obscurus*. Thus Hagen's Monograph adds only a few new localities, namely: for *C. limosus (affinis)* the Schuylkill River, Philadelphia, and Carlisle, Cumberland County. The new locality "Pittsburgh" for the same species is wrong.

The great revision of the genus published by Faxon (1885*a*) adds two species: *C. diogenes* from Derry, Westmoreland County, and *C. rusticus* from Pittsburg. The latter record is incorrect, and should be dropped. Besides Faxon gives the following new localities: *C. limosus*, Brandywine Creek, Chester County; Delaware River, Bristol, Bucks County; Bainbridge, Lancaster County; *C. bartoni*, Bedford and Pattonville, (see *infra*, foot-note 16), Bedford County; Windham, Bradford County; Hummelstown, Dauphin County; Chester County; Bainbridge, Lancaster County; McKean County.

Thus only three species were known up to this date: C. limosus, C. bartoni, and C. diogenes.

In 1898 Faxon added a fourth species for the state, *C. obscurus* from Westmoreland County, and also gave a new locality for *C. bartoni*, Westmoreland County.

Williamson (1901) enumerated five species, and one variety from Allegheny County, but, as has been demonstrated by the writer (1905*a*), this is to be reduced to four species and one variety, of which the species recorded as *C. dubius* by Williamson (*C. monongalensis* Ortmann) is new for the state, as is also the variety *C. bartoni robustus*. Allegheny County is for the first time cited as a locality for the other species, *C. obscurus* (recorded as *C. propinquus* and *rusticus*), *C. bartoni*, and *C. diogenes*. Williamson's discoveries brought up the number of species known from the state to five, and one variety, namely: *C. limosus*, *C. obscurus*, *C. bartoni*, *C. barto*

In the preliminary report of the writer for western Pennsylvania, two other species were added: C. propinquus from Eric and Crawford Counties, and C. carolinus from Fayette, Westmoreland, and Somerset Counties. Numerous new localities were added to those already known. C. dubius of Williamson was recognized as a species new to science, and described as C. monongalensis. The number of species present in the state has not been increased by subsequent investigations, and stands now as seven, with one variety, namely: Cambarus limosus (Rafinesque); C. propinquus Girard; C. obscurus Hagen; C. bartoni (Fabricius); C. bartoni robustus (Girard); C. carolinus Erichson; C. monongalensis Ortmann; C. diogenes Girard.

These eight different forms are treated in the following pages, with the addition of one extralimital form, a variety of *C. propinquus* (*C. propinquus sanborni*). The recent and past observations made by the writer, together with those collated from other sources, are presented as completely as possible in the succeeding pages, thus giving a natúral history of this group of animals, so far as found in the state of Pennsylvania. It has always been the aim of the writer to support his conclusions by evidence secured within the state, but observations made outside of the state are sometimes introduced, where a gap was to be filled, or where they were of special interest.

III. MORPHOLOGY AND CHOROLOGY OF THE PENNSYLVANIAN SPECIES. A. General Remarks.

The crawfishes (as to the use of "crawfish" in preference to "crayfish" see infra, VI) of the state of Pennsylvania belong to the genus Cambarus² of Erichson (1846), of the family Potamobiidæ Huxley, including the freshwater crawfishes of the northern hemisphere. Faxon (1898) regards this as a subfamily, Astacinæ, of the family Astacida, which also includes the subfamily, Parastacina of the southern hemisphere, now regarded as a family, Parastacidæ Huxley. There is some discussion as to the proper name of the family, depending on the use of the generic name Astacus Fabricius, or of Potamobius Samouelle, for the European crawfishes. The position of the writer was defined in 1902, (Proc. Amer. Philos. Soc. XLI, p. 276, footnote). The question, however, has recently been finally settled by a discovery made by Miss M. J. Rathbun (Proc. Biol. Soc. Washington, XVII, 1904, p. 170), but not in the manner suggested by Miss Rathbun. The fact that the name Homarus was used first by Weber (Nomenclator Entomologicus, 1795), in place of Astacus Fabricius, 1775, makes *Homarus* a pure and simple synonym of *Astacus*, and according to the rule "once a synonym, always a synonym," it remains a synonym. There is no reason to make it "desirable," as Miss Rathbun expresses it, to set aside the rule in this case,

The genus *Cambarus*, containing now about 70 species, has been variously subdivided: by Girard (1852) into three groups; by Hagen (1870) likewise into three groups, which, however, do not exactly correspond to those of Girard; and by Faxon (1885a) into five groups. Recently the present writer has divided the genus into six subgenera, namely: *Paracambarus*, *Procambarus*, *Cambarus*, *Cambarellus*, *Faxonius*, *Bartonius*. (See *Proc. Am. Phil. Soc.*, XLIV, 1905, p. 91, *ct seq.*; *Ann. Carn. Mus.* III, 1905, p. 437; and *Proc. Washington Acad. Science*, VIII, p. 1, 1906.)

 2 Erichson made this provisionally a subgenus, but expressed the opinion that it perhaps would better rank as a genus. Girard (1852) was the first to use *Cambarus* as a generic name.

Only the two last named subgenera, *Faxonius* and *Bartonius*, are found within the boundaries of the state of Pennsylvania, and they are distinguished from the rest by the shape of the male copulatory organs. The latter consist of two parts, which are completely separated at the tips for a shorter or longer distance, and never possess any accessory spines. The outer part in the male of the first form, (sexually ripe), is almost completely transformed into a horny spine, while the inner remains soft. In the Pennsylvanian species of these two subgenera only the third pereiopods possess a hook (used to take hold of the female) on the ischiopodite.

The two subgenera are distinguished as follows : Subgenus *Faxonius* Ortmann.

Sexual organs of first pair in the male with two shorter or longer completely separated tips. Tips straight or gently curved, divergent, parallel, or convergent, generally rather slender.

Subgenus Bartonius Ortmann.

Sexual organs of the first pair in the male with two rather short, completely separated tips. Both tips are strongly recurved, forming with the basal part about a right angle.

B. Key to the Pennsylvanian Species of the Genus Cambarus.

- a'. Sexual organs of male of the *Faxonius*-type. Rostrum always with a marginal spine on each side, and carapace with one or more lateral spines. (River species.)
 - b'. Tips of sexual organs short, straight, and divergent. Sides of carapace with several lateral spines anterior to, and behind the cervical groove. (Delaware, Susquehanna, and Potomac drainages.)

C. (Faxonius) limosus (Rafinesque).

- b". Tips of sexual organs long, almost straight, slightly convergent, or parallel. Sides of carapace with only one spine behind the c-rvical groove.
 - e'. Rostrum with median keel. Sexual organs of male of first form at anterior margin without prominent angle (shoulder). Annulus ventralis of female flat. (Lake Erie and its drainage.)

C. (Faxonius) propinquus Girard.

- a'. Sexual organs of male of the *Bartonius*-type. Rostrum always without marginal spines. Carapace generally without lateral spines.
 - b'. Areola wide. Form of carapace depressed. Color brownish or greenish. (Species of the small streams.)
 C. (Bartonius) bartoni (Fabricins).
 - b'. Areola narrow or obliterated in the middle. Form of carapace rather compressed. (Burrowing species.)
 c'. Areola narrow. Inner margin of hand generally with only one row of tubereles. Color very hright, of tints unusual among crawfishes.
 - d'. Color red. Rostrum short and very broad. Outer margin of hand serrated. (Mountains of southern Pennsylvania).
 C. (Bartonius) carolinus Erichson.
 - d". Color blue. Rostrum short and narrower. Outer margin of hand rounded, not serrated. (Hills of southwestern Pennsylvania.)
 C. (Bartonius) monongalensis Ortmann.

e^{''}. Rostrum without median keel. Sexual organs of male of first form at anterior margin with a prominent angle (shoulder). Annulus ventralis of female with two tubercles in anterior part. (Ohio drainage).
 C. (Faxonius) obscurus Hagen.

c". Areola generally obliterated in the middle, or extremely narrow. Inner margin of hand with several rows of tubercles. Color greenish or brownish. Rostrum rather long and narrow. (Swamps on hills and in lowlands, southwestern and eastern Pennsylvania.)
 C. (Bartonius) diogenes Girard.

C. Description and Distribution of the Species.

1. CAMBARUS (FAXONIUS) LIMOSUS (Rafinesque).

(Plate B, Fig. 3; Plate XXXIX, Figs. 5a and 5b.)

Astacus limosus Rafinesque, 1817, p. 4 .

Astacus affinis Say, 1817, p. 168; Harlan, 1835, p. 230, fig. 2; DeKay, 1844, p. 23; Gibbes, 1850, p. 195 (partim). Astacus bartoni Milne-Edwards, 1837, p. 331 (non Fabricius).

Cambarus affinis Girard, 1852, p. 37; Hagen, 1870, p. 60; Pl. 1, figs. 19, 22, 84, 85, Pl. 3, fig. 152, Pl. 5; Abbott, 1873, p. 80; Smith, 1874, p. 638; Faxon, 1884b, p. 146; Faxon, 1885a, p. 86; Faxon, 1885b, p. 360; Underwood, 1886,

p. 366; Faxon, 1890, p. 628; Hay, 1899, p. 960, 964; Andrews, 1894, p. 165.

Cambarus pealei Girard, 1852, p. 87.

Cambarus (Faxonius) limosus Ortmann, 1905b, p. 107, 112, 131.

Body robust, pubescent all over, but chiefly so on carapace and chelæ; but the pubescence wears off easily, and in old individuals, especially in early spring, the body is more or less hairless. The hairs are most persistent on the fingers of the large chelæ.

Carapace subovate, depressed, the depression being brought about by a bulging out of the branchial regions. The vertical height of the carapace, at a point about in the middle of the gastric region (measured from this point to a point on the sternum just in front of the first pereiopods), the vertical height of the carapace at a point of the areola directly above the sternum between the second pereiopods, and the greatest width of the carapace at the hepatic regions are about the same; while the greatest width of the carapace at the branchial regions is distinctly greater. Relation G: H: B = 1:1:1.2 to $1.4.^3$ The greatest width of carapace (at branchial regions) is well behind, at about the middle of the branchial regions. The whole carapace appears rather flattened dorsally.

Cervical groove deep, continuous on the sides. Areola about half as long as anterior section of carapace (including rostrum). Relation of a: p = 1:0.40 to $0.55.^4$ Areola rather broad, relation of w: l = 1:4.0 to $5.4,^5$ with about 5 irregular rows of punctures.

Rostrum long and broad, reaching to the middle of the fifth joint of the peduncle of the antenna, and to the end of the peduncle of the antennula, rarely slightly

 $^{{}^{3}}G$ = vertical diameter at gastric region; H = transverse diameter at hepatic region; B = transverse diameter at branchial region.

a = anterior, p = posterior section of carapace.

 $^{^{5}}w =$ width, l =length of areola.

longer. Surface deeply concave, margins elevated and thickened, almost straight, very little convergent toward the marginal spines. Marginal spines well developed. Acumen long, triangular, acutely pointed, about one third as long as the whole rostrum, sometimes slightly shorter or longer. *Post-orbital ridges* parallel, ending in a sharp spine anteriorly.

Surface of carapace finely punctate, and very finely granulate on the sides in old specimens. Sides spinose. There are a number of larger and smaller spines on each side on the hepatic region, and a few spines are found on the branchial region immediately behind the cervical groove, of which one is generally much larger than the others. (In most cases there are two distinct spines, one above the other, the lower one the larger.) All these spines are well developed only in larger individuals; in young ones only two spines behind the cervical groove and one spine on the hepatic region are present, but these are visible even in the smallest specimens at hand (25 mm. long). External orbital angle not marked, rounded off. Branchiostegal spine sharp and distinct.

Abdomen longer than the carapace, slightly narrower than the carapace in the male, slightly wider in the female. Anterior section of telson on the outer posterior corners generally with two spines, but there may be from one to three; the number of spines may differ on either side. Posterior section of telson semicircular, slightly wider than long, and slightly shorter than anterior section.

Epistoma with posterior part short and broad, almost three times as wide as long, not plane, with a transverse groove posterior to the middle, and an anterior median depression; these are often united into a triangular or arrow-shaped depression. Anterior section constricted at base, its anterior margin almost semicircular, with a small median point, slightly varying in shape (sometimes it is subtriangular, sometimes the anterior point is obscure), but its transverse diameter is always slightly greater than the longitudinal.

Antennula with a sharp spine on the lower margin of the basal joint.

Antennal peduncle with a sharp spine on the outer side of each of the two basal joints.

Antennal scale long, as long as the rostrum or even slightly longer, reaching to the middle or the end of the terminal joint of the antennal peduncle. Outer margin with a strong spine. Laminar part rather broad; its margin more or less regularly curved; the broadest part is in the middle or slightly anterior to it.

Flagellum, when laid backward, reaching to the fourth or even to the middle of the fifth abdominal segment in the male; in the female it generally does not reach beyond the posterior margin of the third segment.

First perceiopods comparatively short, and not very stout, considering the size of the species. Hand short and not very broad, depressed, elongate-ovate, stronger and more elongate in the male than in the female. Surface punctate. Inner margin almost straight, with a double row of tubercles, which are more or less spiniform. Outer margin smooth, bluntly angular, more distinctly so distally. Fingers distinctly longer than the palm (measured from articular tubercle on upper side of carpopodite to articular tubercle on upper side of palm at base of movable finger), straight, cutting edges straight, in contact all along their length, with a few very small tubercles in the proximal part, for the rest without teeth or tubercles, but with a short and dense pubescence, becoming slightly barbate proximally on lower side. Upper surface of each finger with a low longitudinal rib, most distinct distally. Lower surface of hand almost smooth, sparsely punctate.

Carpopolite slightly longer than wide, shorter than palm, punctate. Upper surface with a distinct longitudinal sulcus. Inner margin with a strong procurved spine in the middle, and a small spine anterior to it. Lower surface with two strong spines, one in the middle of the anterior margin, the other at articulation with hand. Sometimes there are additional small spines or spiniform tubercles, proximal to, or above, the large spine of the inner margin.

Meropodite smooth, upper margin with two (rarely more, up to four) strong spines at a short distance from the distal end. Lower margin with two rows of strong spines, the inner one consisting of four to ten spines, largest distally, the outer one of two to three spines. A spine at the outer articulation with the carpopodite.

Ischiopodite of third pereiopods hooked in the male; hook in the male of the first form strong, subconical.

Coxopodites of posterior pereiopods without prominent crests or tubercles in the male.

First pleopods of male of the first form (Plate I, Fig. 5a and 5b) rather strong and short, not reaching beyond the anterior margin of the coxopodites of the third pereiopods. They are not articulated at the base, straight, and the two parts are separated at the tips only for a short distance. Tips crossed (twisted), divergent; that of the inner part is soft, gradually tapering to a point, and is directed obliquely outward; that of the outer part is horny, gradually tapering to a point, and directed obliquely forward and slightly inward.

In the male of the second form the first pleopods are articulated at the base when young, but not articulated when old, and both tips are soft; that of the outer part is rather bluntly pointed.

Annulus ventralis of female transversely rhombiform, with a short transverse groove slightly posterior to the middle, and an S-shaped longitudinal fissure. Anterior to the central groove there is on each side of the fissure a strong, tuberculiform elevation, so that the fissure is situated in a rather deep depression. Posterior to the central groove, there is a slight elevation, over which the fissure passes. The annulus, consequently, appears trituberculate, the two anterior tubercles being stronger than the posterior. In young females, the tubercles are only slightly developed, and generally the posterior tubercle is almost obsolete.

Size. — Rafinesque gives as total length 3–9 inches. The maximum, 9 in., = 229 mm., seems rather strange, since no such specimens have ever been subsequently seen, even if we infer that Rafinesque intended the whole length, including the claws. Hagen (1870, pl. 5) figures a very large female, which, including the outstretched claws, would not be longer than about 7 inches (178 mm.). Its body from the tip of the rostrum to the end of the telson, is 132 mm. long. The maximum length given by Hagen in the text (p. 61) is 4.7 in., =119 mm; thus this figure, although said to be of natural size, is apparently somewhat enlarged.

The largest specimens ever seen by the writer are in the museum of Oberlin College from the Potomac River, a female measuring 120 mm., and a male of the first form measuring 105 mm. The largest specimen from Pennsylvania I possess, is a female from the Delaware River at Torresdale, and measures 93 mm. in length; the largest male (first form) is from the Delaware at Penns Manor, measuring 75 mm. in length. A male of the second form from Holmesburg is 85 mm. long. Specimens over 100 mm. long, mentioned by the writer, (1899, p. 1210), as from Philadelphia, are from the New Jersey side of the river, near Camden.

Colors. —(Plate B, Fig. 3.) An account of the color of this species has been given by Faxon (1885*a*, p. 88). .It runs thus: "Upper surface greenish, mottled with darker green, especially on the chelæ; tips of fingers orange, preceded by a dark green ring, which runs along the outer border of the hand to the wrists; abdominal somites ornamented with interrupted transverse chestnut-colored double bands. Under surface of a lighter hue."

I have repeatedly made notes from live specimens, and have found that the shades of color vary greatly, although the general pattern has been correctly described by Faxon. The general color of the body may be described as *olive-green* (Ridgway, 1×86 , X, $18)^6$, but it varies toward *tawny-olive* (III, 17), and *olive-yellow* (VI, 16). The sides of the carapace are generally lighter, of a whitish green.

⁶ In the description of colors, I have used here (and in the following species) the nomenclature of Ridgway (1886), and the Roman and Arabic numerals refer to his plates and figures.

There is a brown (chestnut, IV, 9) spot on the anterior margin of the carapace on each side below the eyes, not noticed by Faxon. The brown bands of the abdomen are burnt sienna (IV, 6). In the middle of the abdomen the epimera are hazel (IV, 12). The color of the finger tips is *ferrugineous* (1V, 10), often paler, the preceding band is dark olive-green, often almost black. The articular tubercles on the lower side of the hand are tawny (V, 1), on the upper side they are dark-green. The articular membranes of the chelæ are wine-purple (VIII, 15). The darker green of the carapace is generally confined to distinct large blotches, symmetrically disposed; one pair on the gastric region, and one each on the anterior and the posterior part of the branchial regions. Often the two blotches of the gastric region run together, which may also be the case with those of the branchial regions. They often appear spotted or mottled with the lighter, or rather more brownish (tawny olive), ground color. The brown spot on the anterior margin of the carapace is sometimes indistinct, and in young specimens with fresh shells, it may have a trace of yellow below. All these colors are bright and distinct only in fresh shells. On old shells, a coat of mud is generally deposited, giving to the whole body a dirty blackish color, and besides, the colors themselves fade considerably, so that only a dirty olivegreen remains, with some brown on the abdomen.

The color of newly laid eggs under the abdomen of the female is *olive-green* (X, 18).

The above description is founded upon the examination of one hundred and twenty-one specimens, now preserved in the collections of the Carnegie Museum. Fifty-six of these specimens are from the state of Pennsylvania, fifty-four from New Jersey, eight from Maryland, and three from West Virginia (Potomac River at Cherry Run, Morgan County). This, however, does not represent the total number of specimens seen by the writer, since many others were collected by him, as well as seen in the collections of the Department of Agriculture of Pennsylvania, of the Academy of Natural Sciences in Philadelphia, and of Oberlin College.

DISTRIBUTION.⁷

LOCALITIES REPRESENTED IN THE COLLECTIONS OF THE CARNEGIE MUSEUM.

PENNSYLVANIA: Bucks Co., Delaware River, New Hope; Delaware River, Penns Manor; Little Neshaminy Creek, Grenoble; Common Creek, Tullytown; Philadelphia Co., Delaware River, Torresdale Fish Hatchery, Torresdale; Delaware

⁷ All localities without further record have been ascertained by the writer in person. In other cases the authority (when published), or the collector and institution, where the specimens are preserved, is given.

River, Holmesburg, (H. W. Fowler coll., exch. Acad. Phil. Nat. Sci.); Schuylkill Canal, Manayunk; *Montgomery Co.*, Schuylkill River, West Manayunk, (H. Gera coll.); *Delaware Co.*, Marcus Hook Creek, Marcus Hook; *Franklin Co.*, Back Creek, Williamson; *Bedford Co.*, Raystown Branch of Juniata River, Bedford (A. Kœnig coll.).

NEW JERSEY: Camden Co., Delaware River, Camden; Delaware River, North Cramer Hill; Mercer Co., Stony Brook, Princeton; Delaware-Raritan Canal, Aqueduct near Princeton.

MARYLAND: Alleghany Co., Potomac River, Wiley's Ford, South Cumberland. WEST VIRGINIA: Morgan Co., Potomac River, Cherry Run.

PREVIOUS RECORDS.8

Type locality : Delaware River, Philadelphia, (Rafinesque).

PENNSYLVANIA: Schuylkill River, Philadelphia, (Hagen); Bucks Co., Bristol, (Faxon); Berks Co., Schuylkill River, Reading, (Girard); Chester Co., Brandywine Creek, (Faxon); Tributary of Brandywine Creek, Chadds Ford Junction, (Ortmann); Lancaster Co., Bainbridge, (Faxon); Cumberland Co., Carlisle, (Hagen); Adams Co., Gettysburg, (Ortmann).

NEW JERSEY: Camden Co., Camden, (Faxon); Burlington Co., Burlington, (Faxon); Mercer Co., Trenton, (Abbott); Monmouth Co., Red Bank, (Faxon); Morris Co., Schooley's Mountain, (Faxon).

MARYLAND: Cecil Co., (Faxon); Hartford Co., Havre de Grace, (Hagen); Baltimore Co., Baltimore, (Andrews); Guynn's Falls, (Faxon); Druid Hill, (Faxon); Anne Arundel Co., (Faxon); Charles Co., (Faxon); Montgomery Co., (Faxon); Washington Co., Williamsport, (Faxon); Alleghany Co., Canal four miles south of Cumberland, (Faxon).

DISTRICT OF COLUMBIA: Washington, (Girard).

VIRGINIA: *Fairfax Co.*, Gunston, (Faxon); *Augusta Co.*, Shenandoah River, Waynesboro, (Faxon); *Isle of Wight Co.*, Blackwater River, Zuni, (Faxon).

NEW LOCALITIES NOT REPRESENTED IN CARNEGIE MUSEUM.

PENNSYLVANIA: Montgomery Co., Roberts Run, Abrams, (B. W. Griffiths & H. W. Fowler, coll., Acad. Nat. Sci., Philadelphia),

The following records are from the collections of Mr. W. R. McConnell, belonging to the Department of Agriculture, Harrisburg: Yellow Breeches Creek, New Cumberland, Cumberland Co.; Conedogwinet Creek, West Fairview, Cumberland Co.; Sherman's Creek, Landisburg, Perry Co.; Montour Run, Greenpark, Perry

⁸ A number of doubtful records have been dropped (see Ortmann, 1905b, p. 131). Too general records are also omitted, for instance: "Susquebanna River, Pa., (Faxon)," since just in this case more exact information is desired.

Co.; Susquehanna River, Northumberland, Northumberland Co.; Fishing Creek, Bloomsburg, Columbia Co.; Bald Eagle Creek, Milesburg, Center Co.; Conococheague Creek, Chambersburg, Marion, and Williamson, Franklin Co.; Maiden Creek, Maiden Creek, Berks Co.

REMARKS.

Cambarus limosus is the common river species of eastern Pennsylvania. Its morphological characters are very constant, and give it a rather isolated position within the genus, which is also expressed by, and very likely due to, its geographical isolation, the most closely allied species being found far to the west, in Indiana and Kentucky, (see Ortmann, 1905b, p. 114, 127). The most prominent specific characters are furnished by the male sexual organs, and the spinosity of the sides of the carapace. The description, as given above, does not indicate any important variations, and the specimens are generally very uniform. The spinosity of the carapace, however, changes with age, young specimens being much less spinose than old ones. In the spines of the chelipeds and of the anterior section of the telson, there is some variation, but this is only slight and not subject to any rule. The shape of the carapace and rostrum is very constant, the only differences of age noticed are found in the acumen of the rostrum, which in young specimens is slenderer than in those which are older, and in the bulging out of the branchial regions of the carapace, which is most marked in old individuals. The changes in the pubescence of the whole body are apparently due to wear. The short hairs generally present in newly moulted individuals slowly wear off, and specimens with a distinct coat of dirt upon them, indicating age, generally have the pubescence more or less, sometimes entirely, worn off. Only on the hands and fingers are traces of it left.

I myself have never found any freaks in this species. But Mr. W. R. McConnell found a male (first form), 66 mm. long, at Bloomsburg, Columbia County, (the only specimen taken at this locality), in which the rostrum had two pairs of marginal spines. The additional pair in this specimen is smaller, and stands about midway between the normal pair and the base of the rostrum.

2. CAMBARUS (FAXONIUS) PROPINQUUS Girard.

(Plate XXXIX, Fig. 6a and 6b.)

Cambarus propinquus, Girard, 1852, p. 88; Hagen, 1870, p. 67, Pl 1, f. 34-38, Pl. 3, f. 1.3; Smith, 1874, p. 638; Forbes, 1876, p. 4, 19; Bundy, 1877, p. 171; Bundy, 1882, p. 181; Bundy, 1883, p. 402; Faxon, 1884, p. 147; Faxon, 1885a, p. 91; Faxon, 1885b, p. 360; Underwood, 1886, p. 371; Faxon, 1890, p. 628; Hay, 1896, p. 497, Fig. 11; Ward, 1896, p. 15; Faxon, 1898, p. 651; Hay, 1899, p. 960, 962; Ortmann, 1905a, p. 400.

Cambarus (Faxonius) propinquus Ortmann, 1505b, p. 112, 132.

Body not very robust, not pubescent, with only a few, scattered, short hairs, chiefly on the chelæ, but the hair wears off very soon, and the body becomes smooth, with exception of a slight pubescence at the base of the cutting edges of the fingers.

Carapace subovate, depressed. Relation G: H: B = 1:1:1.2 or 1.3. (The width of the branchial regions appears slightly less than in *C. limosus*, but this is probably due to the fact that the specimens of *C. propinquus* at hand are rather small). Greatest width of branchial regions well behind, at about the middle of the branchial regions. Carapace flattened dorsally.

Cervical groove deep, more or less distinctly interrupted on the sides just above the lateral spine. Posterior section of carapace about half as long as anterior (relation a: p = 1:0.42 to 0.62.

Areola rather broad, w: l = 1:4.7 to 6.0, with about four irregular rows of punctures.

Rostrum long and broad, reaching to the middle of the fifth joint of the peduncle of the antenna, and to the end of the peduncle of the antennula, sometimes slightly shorter. Surface concave, with a more or less distinct, low, longitudinal median keel toward the tip. Margins elevated, but not much thickened, straight, more or less convergent toward the marginal spines. Marginal spines generally well developed in young specimens, less so in older ones, sometimes quite small. Acumen long, triangular, comparatively longer in young specimens, pointed, about one-third as long as the whole rostrum, or shorter. Postorbital ridges slightly divergent posteriorly, ending anteriorly in a more or less distinct small spine.

Surface of carapace finely punctate, and slightly granulate on the hepatic regions in old specimens. Sides with only one spine on the branchial regions, immediately behind the cervical groove. This spine is always present and sharp, but generally not very large. No other spines on the sides of the carapace. External orbital angle not marked. Branchiostegal spine small, but sharp, or tuberculiform, or even obsolete.

Abdomen longer than carapace, slightly narrower than the carapace in the male, about as wide as the latter in the female. Anterior section of telson on the outer posterior corners with one to three spines (two spines is the general condition). Posterior section of telson semielliptical, considerably wider than long, and slightly shorter than anterior section.

Epistoma with posterior part short and broad, almost three times as wide as long, not plane, with a transverse groove and an anterior median depression running into each other. Anterior section constricted at base, its anterior margin generally almost semicircular, with a median point and an indistinct angle on each side, but shape rather variable: sometimes it is truncate anteriorly, with or without median point,

the lateral angles being more distinct. Its transverse diameter is slightly greater than the longitudinal.

Antennula with a distinct, sharp spine on the lower margin of the basal joint. Antennal peduncle with a distinct spine on the outer side of the first joint, and a smaller, sometimes tuberculiform spine on the second joint. Antennal scale long, as long as rostrum or slightly longer, reaching to the middle, or almost to the end of the terminal joint of the antennal peduncle. Outer margin with a strong spine. Laminar part rather broad, almost semicircular, the broadest part is slightly anterior to the middle.

Flagellum reaching to the beginning of the fifth abdominal segment in both the male and the female.

First percoopds not very robust, comparatively longer in the male, shorter in the female. Hand elongate-ovate, depressed, moderately wide. Surface punctate. Inner margin almost straight, with a double row of tubercles. Outer margin smooth, marginated and bluntly angular, but almost evenly rounded near the proximal end. Fingers longer than palm, almost straight in the female, and meeting all along their edges; in the male, the fingers are slightly gaping at the base, and the movable one is slightly curved in the shape of an "S," which curve is chiefly noticeable along the outer margin. Outer margin of movable finger slightly tuberculate at base. Cutting edges with a few small tubercles near the base, for the rest slightly pubescent. Upper surface of each finger with a low, longitudinal rib. Lower surface of hand sparsely punctate.

Carpopolite slightly longer than wide, shorter than palm, punctate, and with a longitudinal sulcus on upper side. Inner margin with a strong, slightly procurved spine in the middle; generally there is a tubercle (rarely spiniform) anterior to this spine. Lower surface with a low and broad tubercle in the middle of the anterior margin, which is very rarely subspiniform; a similar tubercle with a spiniform tip at the articulation with the hand. No other spines or tubercles on the carpododite, except that sometimes there is a small tubercle at the proximal end of the inner margin.

Meropodite smooth; upper margin with two small, often indistinct, or tuberculiform, spines near the distal end. Lower margin with two rows of spines; the outer row consisting of only one, rarely of two, spines; the inner row consisting of a large distal spine, and a number (up to seven or eight) of very small ones, which may be entirely absent. Thus there are often only two anterior spines present, representing the distal spine of each row. A small spine at the outer articular tubercle with carpopodite.

Ischiopodite of third pereiopod hooked in the male, the hook in the male of the first form being strong, subconical.

Coxopodites of posterior pereiopods without prominent crests or tubercles in the male.

First pleopods of male of the first form (Plate XXXIX, Fig. 6a) slender, but rather short, hardly reaching beyond the middle of the coxopodites of the third pereiopods. They are not articulated at the base, and the two parts are completely separated at the tips for a rather considerable distance (about one third of the length from the inner basal tubercle to the tip). Both parts are almost parallel, only slightly convergent at the tips, which is due to a very slight curve of the outer part. Outer part gradually tapering from base to tip, horny. Inner part soft, of about the same shape as the outer, and of the same length, gradually tapering to an acute tip. Both parts are slightly twisted, so that the tip of the outer is directly anterior to that of the inner. Anterior margin of this organ without shoulder shortly below the point of separation of the two parts; sometimes, indeed, there is a slight notch, but never a sharp shoulder.

In the male of the second form, the first pleopods (Plate XXXIX, Fig. 6b) are articulated at the base when young, (only young specimens are at hand); both parts are separated only for a short distance, and are soft; the outer one is rather blunt, while the inner one tapers to a point. No notch or shoulder on anterior margin.

Annulus ventralis of female transversely rhombiform or ovate, rather flat, very slightly depressed in the middle, with an S-shaped longitudinal fissure. No tubercles on anterior part. In young females, the median depression is very indistinct, and the annulus is almost eompletely flat.

Size. — Hagen gives 2.6 in. = 66 mm. as the maximum length for this species. The largest individuals from the state of Pennsylvania observed by the writer, are a male (first form) from Albion, Erie County, 61.5 mm. long, and a female from the same locality 69 mm. long. I have seen, however, two larger males (first form) from Lake Erie, off the shore of Lorain County, Ohio (Mus. Oberlin), one measuring 77 mm., the other 81 mm. in length. Nevertheless, this seems to be one of the smaller species, for in the streams running to Lake Erie in Pennsylvania a considerable number of individuals have been taken, none of which was longer than the above mentioned specimens.

Colors. — The colors of this species agree closely with those of *C. obscurus* (which see for further particulars). The following notes were taken from an adult female, eollected on the shore of Lake Erie at Miles Grove.

General color, olive-green (Ridgway, 1886, X, 18), sides of carapace cream-color (VI, 20). A rufous (IV, 7) spot on anterior margin of carapace. Lower side whitish. Anterior half of abdominal segments hazel (IV, 12). Chelæ olive-yellow (VI, 16), mottled with olive-green. Finger tips orange (VI, 3), followed proximally by a citron-yellow (VI, 15) band. One rufous articular tubercle above on the hand. Articular membranes of hand lake-red (VII, 2). Finger tips of chelæ of second and third pereiopods, and dactylopodites of fourth and fifth pereiopods orange. Pereiopods pale brownish-white, mottled and marbled with olive-yellow. Antennal flagellum annulated olive-green and ochraceous (V, 7). Spines on sides of carapace and rostrum buff (V, 13). Antennal scale olive-yellow, its center olive-green.

It is to be remarked that in this specimen no dark olive-green band is found near the finger-tips. The same was the case generally in specimens from Temple Creek, Albion, and from Elk Creek (all collected in autumn). However, specimens from Conneautville Station, Crawford County, collected in June, generally had a dark green, almost black band, succeeding the pale band. A similar dark band appeared in some of the Temple Creek specimens, after they had been preserved for some time in alcohol, but it disappeared again with the progress of the bleaching action of the preserving fluid. In collecting the specimens of this species and of *C. obseurus* in Erie County in October, 1904, I was generally able to distinguish the two species, where they were found associated, by the color of the finger tips. However, too much reliance should not be placed upon this character, since I was not subsequently able to test this observation.

The description of this species, as given above, is drawn from sixty-one specimens preserved in the collection of the Carnegie Museum. Of these, fifty-three are from the State of Pennsylvania (forty-eight from streams flowing into Lake Erie, five from the lake itself). One specimen is from Lake Erie, Erie County, Ohio, and seven are from the northern parts of Michigan.

DISTRIBUTION (see Plate XLII, Fig. 3).

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: *Erie County*, Lake Erie, Presque Isle, (D. A. Atkinson coll.); Lake Erie, Miles Grove; Walnut Creek, Swanville; Elk Creek, Girard; Elk Creek, Miles Grove; Conneaut Creek, Albion; Temple Creek, Albion; *Crawford County*, tributary of Conneaut Creek, Conneautville Station.

Оню: *Erie County*, Lake Erie, Cedar Point, near Sandusky, (O. E. Jennings coll.).

MICHIGAN: *Emmet County*, Crooked Lake, Oden near Petoskey, (E. B. Williamson coll.).

PREVIOUS RECORDS.⁹

Type locality: Oswego, Oswego County, New York, (Girard).¹⁰

CANADA: Montreal, Quebee, (Faxon); Toronto, Ontario, (Faxon).

NEW YORK: St. Lawrence County, Grass River, (Hagen); Canton, (Faxon); Blaek Lake, (Faxon); Ogdensburg, (Faxon); Jefferson County, Garrison Creek, Sackett's Harbor, (Girard); Oneida County, Oneida Lake, (Hagen); Cayuga County, Cayuga Lake, (Faxon); Monroe County, Rochester, (Hagen); Niagara County, Niagara-(Hagen); Chautauqua County, Forestville, (Faxon).

Оню: Lorain County, Lake Erie, (Ortmann); Ottawa County, Portage River, Oak Harbor, (Faxon).

MICHIGAN: Wayne County, Detroit River, (Faxon); Northville, (Faxon); Eeorse, (Faxon); Washtenaw County, Ann Arbor, (Faxon); St. Clair County, St. Clair River, (Faxon); Calhoun County, Marshall, (Faxon); Allegan County, Otsego, (Faxon); Saginaw County, Saginaw River, (Faxon); Charlevoix County, Lake Miehigan, Round and Pine Lakes, Charlevoix, (Ward).¹¹

INDIANA: De Kalb County, Waterloo, (Hay); Noble County, Rome City, (Bundy); Kosciusco County, Turkey Lake, (Hay); Marshall County, Maxinkuehee Lake, (Hay); Twin Lakes, (Hay); Laporte County, Miehigan City, (Faxon); Carroll County, Delphi, (Hagen); Tippecanoe County, Lafayette, (Faxon); Marion County, Indianapolis (Faxon); Irvington (Hay); Millersville (Hay); Franklin County, Brookville (Hay); Brown County, Salt Creek (Hay); Monroe County, Clear Creek, Bloomington (Faxon); Greene County, Switz City (Faxon); Sullivan County, Turman Creek (Faxon).¹²

ILLINOIS: Macon County, Deeatur (Faxon); McLean County, Normal (Forbes); Tazewell County, Pekin (Forbes); Kane County, Geneva (Faxon); Ogle County, (Hagen); Stephenson County, Freeport (Forbes).¹³

WISCONSIN: Greene County (Faxon); Dane County, Madison (Faxon).

Iowa: Scott County, Davenport (Faxon); Wapello County, Ottumwa (Faxon).

New locality, not represented in Carnegie Museum: Speneerport, Monroe Co., New York, (Mus. Oberlin).

⁹I have omitted "Lake Superior" (Hagen), as unconfirmed (see Ortmann, 1905b, p. 132), and "Green River, Edmonson Conuty, Ky." (Hay, 1802a, p. 235), as doubtful, being founded upon young specimens only.

¹⁰This is the first locality given by Girard, and consequently is the type locality.

¹¹ Faxon gives also from "Michigan": "St. Mary's Lake"; "Mouth of Battle Creek"; and "Lake Douglass." I have not been able to locate these.

¹²Faxon gives in addition : "White River, Indiana" (southeastern section, tributary to Ohio.)

¹³ Faxon gives also : "Aux Plains River, Illinois," which I have not been able to locate.

REMARKS.

Cambarus propinquus in Pennsylvania belongs to Lake Erie and its drainage. The range being rather restricted, the material at hand is not very rich, and its study does not promise many results as to variation. Nevertheless there are a few striking facts, which may be mentioned. In the first place one of the chief specific characters, the longitudinal keel of the rostrum, is decidedly variable. All specimens at hand from outside of the state (eight) show a keel plainly, but this is not so with the Pennsylvanian specimens. The keel in these is often distinct, but shows a tendency to disappear. This is chiefly the case in young individuals, where the rostrum is comparatively narrower, the marginal spines are sharper, and the acumen is slenderer than in older individuals.

The armature of the chelipeds is also rather variable. There is always a strong spine in the middle of the inner margin of the carpopodite, and invariably a small tubercle anterior to it, which in young specimens is often spiniform. Sometimes there is also a small tubercle at the proximal end of the inner margin, but I have generally found this only in larger individuals. The lower side of the carpopodite, as a rule, has only one spine, located at the articulation with the hand, and this is present in all Pennsylvanian specimens I have seen. The anterior margin is often without any spine, or even tubercle; there is, however, a low tubercle developed in many cases, and in two cases it was spiniform, viz., in a male (second form) from Elk Creek, Miles Grove, and in a female from Presque Isle. Both of them had a distinct keel on the rostrum, so that they undoubtedly belong to this species. The rows of spines on the lower margin of the meropodite are generally represented by only two spines, the distal spine of each row being alone present. But it is remarkable that in the set from Conneautville Station, composed of twelve individuals, ten show an increase of the spines of the inner margin, from four to eight little teeth being present behind the large distal spine, while in eight specimens an additional smaller spine is found behind the distal spine of the outer margin. In every case this occurs only on one side, while the other side is normal. A similar increase of the number of spines of the meropodite is also to be observed in a few specimens from Temple Creek, Albion, in the two specimens at hand from Elk Creek, Miles Grove, in the female from Presque Isle, mentioned above, and in the specimen (female) from Sandusky, Ohio. Since the latter has also a spine on the anterior margin of the lower side of the carpopodite, the tendency to develop additional spines may extend simultaneously to carpopodite and meropodite.

The set of seven specimens from northern Michigan is remarkable for the fact

that in no case is there a spine on the carpopolite at the lower articulation with the hand, but only a tubercle; in other respects they are typical, with a spine and anterior tubercle on the inner margin of the carpopolite, a low tubercle at the anterior margin of the lower side of the carpopolite, and only two spines on the lower margin of the meropolite.

In the shape of the sexual organs of the male there is much uniformity in their length and the shape of the tips. However, there is a tendency in the Pennsylvanian specimens toward the development of a slight notch on the anterior margin in the place where *C. obscurus* has a shoulder. I have only twelve males of the first form from Temple Creek, Albion, four from Walnut Creek, and two from Elk Creek. Of these, six from Temple Creek and one from Walnut Creek show a notch, while all the rest (eleven) have no trace of it. The notch never assumes the shape of the "shoulder" of *C. obscurus*, and the sexual organs differ in other respects from the later species, chiefly in that the tip of the inner part is never blunt or dilated.

The female annulus is rather constant, as has been said above; only slight differences due to age are noticeable.

We may sum up the variations of *C. propinquus* in the state of Pennsylvania by saying that there is a distinct inclination toward *C. obscurus*, indicated by the tendency of the rostral keel to disappear, of the chelipeds to increase in spinosity, and of the male copulatory organs to develop a notch at the anterior margin. Nevertheless there are numerous specimens which represent the typical *C. propinquus*. This fact is to be borne in mind, and we shall learn more about it when we come to discuss the geographical distribution of this and the related forms.

I introduce here the systematic account of a variety of this species, which is extralimital to the state of Pennsylvania. I have, however, decided to treat of it more fully, since its relation to the representative Pennsylvania form is highly interesting, and since we shall have to refer to it repeatedly in the chapter on distribution.

2a. CAMBARUS (FAXONIUS) PROPINQUUS SANBORNI (FAXON).

Cambarus sanborni Faxon, 1884b, p. 128.

According to Faxon, this variety differs from the typical *C. propinquus* in the following characters: 1) The two parts of the male sexual organs are less deeply separated, and the tips are closer together. 2) The rostrum is not carinate. 3) The hands are finely public ent. 4) The inferior median anterior spine of the carpopodite is evident.

Cambarus propinquus sanborni Faxon, 1885a, p. 91, Pl. 5, f. 3, Pl. 9, f. 10; Underwood, 1886, p. 372; Osburn & Williamson, 1898, p. 21; Williamson, 1899, p. 20, 48; Hay, 1899, p. 960, 964; Ortmann, 1905b, p. 132,

I possess five specimens (obtained by exchange from Oberlin College) from one of the two localities originally mentioned by Faxon for this form (Oberlin, Ohio), which agree well with his account, with the exception that the pubescence of the hands is not developed; there are, indeed, a number of short hairs in some, chiefly the younger, specimens, implanted in the punctures, but such are also very frequently present in *C. propinquus* (as well as in *C. obscurus*). These hairs are generally present in new, recently moulted specimens, but wear off with age.

The male copulatory organs are very similar in shape to Faxon's figure, although they vary slightly with reference to the length of the separated tips. In this respect, however, the variety is closer to the typical form than to *C. obscurus*. In addition, I notice in the two males of the first form of this set that the inner part of the male organs, although it tapers to a point on a side view, is different on a posterior view. From behind it is broadly and bluntly rounded off, a fact which is due to a marked compression and flattening in an anteroposterior direction toward the tip. This is also the case in the male of the second form at hand. Here both tips of the sexual organs are blunt, that of the inner part less so than that of the outer. I cannot see that the tips of the male organs, either in the first or in the second form, are closer together than in *C. propinquus*.

The armature of the chelipeds in these specimens is slightly different from that of the typical *C. propinquus*, although similar variations have been observed in the latter. In all five specimens there are two distinct spines on the lower side of the carpopodite, one at the articulation with the hand, the other on the anterior margin. The inner margin of the carpopodite, besides the one strong spine, has a distal and a proximal tubercle, and in the two largest individuals (male and female) there are a few additional tubercles on the upper surface of the carpopodite. The inner lower margin of the meropodite invariably has in these specimens behind the distal spine a row of small teeth, becoming spiniform in the larger individuals. The number of teeth in this row is from six to eight. In two specimens the outer lower margin possesses a small tubercle behind the distal spine of each cheliped. In one specimen there is only a tubercle on the right side, and two others have only the distal spine.

In addition to the above specimens from Oberlin I have seen among the Oberlin collections other specimens from the state of Ohio, and have myself collected in eastern Ohio and northern West Virginia a number of specimens, which undoubtedly belong to the same form. The characters are practically the same, and only a few remarks are necessary.

1. The keel of the rostrum is invariably lacking. There is not a single individual which shows any trace of it.

2. The hand of the adult male of the first form has a distinct tendency to become broader than in the typical *propinquus*. This is well shown in the largest male from Oberlin. However, this may be due to the fact that the specimens of this variety at hand are larger than those of the typical form. I notice, however, in specimens from the Tuscarawas drainage and from West Virginia, a tendency in old specimens, chiefly males, to develop on the upper surface of the hand, near the double row of tubercles of the inner margin, additional low tubercles. These may be scattered over the inner half of the surface, or a few of them (3-5) may form an indistinct row between the upper articular tubercle with the carpopolite and the articular tubercle with the dactylopodite. This is a distinct approach toward C. *obscurus*, where similar tubercles are present in larger individuals.

3. The two spines of the lower side of the carpopolite are almost always well developed. There are a number of specimens where they are only bluntly spiniform, or even tubercular, but this is apparently due to wear, a large number of the specimens at hand having been collected in spring, and possessing old worn shells, which had gone through the winter. In a few cases the tubercle on the anterior margin is barely indicated, but all these are cases of regenerated chelæ, as indicated by their size. The armature of the inner margin of the carpopodite entirely corresponds to the Oberlin specimens, old specimens developing additional tubercles on the upper side. A large female from Middle Island Creek, W. Va., has on the left carpopodite a small, but sharp, accessory spine behind the large median spine.

4. The armature of the meropodite is similar to the Oberlin specimens. There is always a series of small teeth behind the anterior spine of the inner lower margin (in old shells they may be indistinct, due to wear); the outer lower margin has an anterior spine, and often a tubercle or a small spine behind it. The latter is very frequent in specimens from the Tuscarawas basin, while in those from the tributaries of the Ohio in West Virginia it is rare; nevertheless, in the large female from Middle Island Creek this second spine is very prominent on the left meropodite.

5. The male copulatory organs are of the *propinquus*-type, that is to say, without a shoulder. There is, however, a distinct tendency, not noticed in the Oberlin specimens, to develop at the anterior margin a small notch in the male of the first form, and it seems that this tendency increases in specimens taken toward the south. Out of ten males of the first form collected at Canton, Ohio, five have no trace of this notch, two have a slight curve in its place, and three show it clearly. This notch in these cases never assumes the shape of a "shoulder." In specimens from Conotton Creek in Harrison and Carroll Counties, Ohio, (only a few males of the first form are at hand), no notch was observed. But out of thirteen males of

the first form collected in Fishing Creek, West Virginia, only two had no trace of it; six had a curve developed in its place, and in five others it was distinct, in one or two representing a blunt angle. The length of the tips of this organ varies slightly, but it is generally less than in *C. obscurus*. The tip of the inner part always corresponds to that of the Oberlin specimens, being compressed and rounded off.

6. The annulus of the female is always of the *propinquus*-type, that is to say, flat, with no tubercles. In old females it becomes a little uneven, the anterior and posterior parts being slightly swollen, but there are never two distinct tubercles as is the case in *C. obscurus*.

We may condense the varietal characters of this form as follows :

C. propinguus sanborni clearly is nearer to propinguus than to C. obscurus on account of the lack of a distinct shoulder on the anterior margin of the copulatory organs of the male of the first form, on account of the general shape and size of this organ, and further, on account of the flat female annulus. It differs from C. propinguus in the flattened and rounded tip of the inner part of the male organ, in the lack of a median keel on the rostrum, and in the shape and armature of the chelipeds, although the latter differences are slight and not always reliable. Just in the latter characters, and in the tendency to develop a notch on the anterior margin of the male organ, it inclines toward C. obscurus. Thus it is clearly a transitional form toward C. obscurus of western Pennsylvania, and its geographical distribution, as we shall see below, is also intermediate between C. propinguus and C. obscurus.

The colors of *C. sanborni* agree throughout with those of *C. propinquus* and *C. obscurus*. The color of the newly laid eggs is dark olive-green, sometimes almost black.

There are one hundred and sixteen specimens of this variety at hand; five are from the Lake Erie drainage in northern Ohio; eighty-one from the Tuscarawas drainage in eastern Ohio, and thirty from Fishing and Middle Island Creeks in West Virginia.

DISTRIBUTION.

(See Plate XLII, Fig. 3.)

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

OHIO: Lorain County, Waterworks Reservoir, Oberlin (R. L. Baird coll., exch. Mus. Oberlin); Stark County, West Branch of Nimishillen Creek, Canton; Carroll County, Conotton Creek, New Hagerstown; Harrison County, Conotton Creek, Bowerstown; Tuscarawas County, Dennison (V. Sterki coll.).

WEST VIRGINIA: Wetzel County, Fishing Creek, New Martinsville; Pleasants County, Middle Island Creek, St. Marys.

PREVIOUS RECORDS.

Type locality : Smoky Creek, Carter County, Kentucky (Faxon).

Оню: Lorain County (Faxon); Vermilion River; Beaver Creek; French Creek (Ortmann); Wayne County, Killbuck Creek, Creston (Ortmann); Tuscarawas County, Tuscarawas River, Gnadenhütten (Ortmann); Knox County, Big Jelloway Creek (Osburn and Williamson); Licking County (Williamson); Franklin County, Alum Creek (Osburn and Williamson).

3. CAMBARUS (FAXONIUS) OBSCURUS Hagen.

(Plate A, Fig. 1 and 2; Plate XXXIX, Fig. 7a-7e; Plate XL, Fig. 1.)

Cambarus obscurus Hagen, 1870, p. 69, Pl. 1, f. 72-75. Pl. 3, f. 154; Smith, 1874, p. 639; Faxon, 1884b, p. 148; Faxon, 1898, p. 652; Ortmann, 1905a, p. 402.

Cambarus propinquus obscurus Faxon, 1885a, p. 92; Faxon, 1885b, p. 360; Underwood, 1886, p. 372; Hay, 1899, p. 960, 964.

Cambarus propinquus and C. rusticus Williamson, 1901, p. 13.

Cambarus (Faxonias) obscurus Ortmann, 1905b, p. 112.

Body of the same shape as in *C. propinquus*, but slightly more robust in old specimens.

Carapace similar to C. propinquus, but the width of the hepatic, as also of the branchial regions, is slightly greater; G: H: B = 1:1.1:1.3 to 1.5. These differences of dimension may, however, be due to the fact that large individuals of this species are at hand.

Cervical groove and *areola* identical with those of *C. propinquus*, but the areola generally is slightly longer than half of the anterior section of the carapace.

Rostrum similar to that of *C. propinquus*, but always without any trace of a median keel. In young specimens the rostrum and its acumen are about identical in shape with those of *C. propinquus*. In older specimens there is a tendency to a shortening of the acumen, which often reaches only to the distal end of the second joint of the peduncle of the antennula and to the base of the terminal joint of the peduncle of the antennula spines in old individuals are often very small and indistinct, represented by mere angles. The postorbital ridges are as in *C. propinquus*.

The punctures and spines of the carapace are identical with those of C. propinguus.

The abdomen, epistoma, antennula, and antenna are also similar to those of C. propinguus.

The first pereiopods (Plate XL, Fig. 1) are generally more robust than in *C. propinquus*, particularly in adult males. Hand wider and more distinctly depressed. The fingers more widely gaping in old males, and the S-shaped curve of the movable finger more pronounced; in old females there is also a slight gap at the base of the fingers. The upper surface of the hand possesses, particularly in large specimens, a small number of scattered low tubercles near the inner margin, and very often (but not always) there is a row of 3–5 tubercles running toward the base of the movable finger, parallel to the inner margin. Tubercles of the outer margin of the dactylopodite more pronounced. The sculpture of the hand is rather variable, and most distinctly developed in old males. The shape of the hand is rather different in the male and female; in the female the fingers are shorter, less gaping (or not at all), rendering the outline of the hand more regularly ovate. (See Plate A, Figs. 1 and 2.)

The *carpopolite* differs from that of *C. propinquus* in the development of a strong tubercle on the anterior margin of the lower side. This tubercle very rarely is indistinct (chiefly so in regenerated claws); generally it ends in a distinct, stout, conical spine. On the inner margin and on the upper face additional low tubercles are not infrequently found.

The *meropodite* differs from that of *C. propinquus* by the constant presence of a series of 4–8 small tubercles, or teeth, behind the distal spine on the inner lower margin. These teeth are never wanting in any of my specimens. The outer lower margin has one or two spines. The latter number is comparatively rare. In regenerated claws very often there is no spine at all on the inner lower margin.

The other characters of the pereiopods are similar to those of C. propinquus.

The first pleopods of male of the first form (Plate XXXIX, Figs. 7a and 7b) are of the general type of those of *C. propinquus*, but slightly longer, reaching to the anterior margin of the coxopodites of the third pereiopods. The inner part does not gradually taper to the tip, but is of nearly uniform thickness, with the tip rounded off and slightly compressed in the antero-posterior direction. Sometimes the tip is even slightly thickened. The anterior margin of this organ, at a point somewhat below the separation of the two parts, has a rather sharp, well marked shoulder, which is absent in none of the specimens at hand (several hundred).

In the male of the second form (Plate XXXIX, Fig. 7c) this shoulder is missing, and the inner part is blunt, similar in shape to the male of the first form, and not tapering to a point as in the typical C. propinguus.

The annulus ventralis of the female has the general shape of that of *C. propin*quus, but the depression in the middle is well marked, and the anterior part has two distinct, subconical tubercles. The posterior part is also elevated into a flat and low tubercle. These tubercles are less distinct in young specimens, but always well developed in females of medium and large size.

Size. — Hagen gives the length as 3.5 in. = 89 mm. The largest individual at hand is a female from Pucketta Creek, Allegheny County (Atkinson coll.), which measures 93 mm. in length. The largest male of the first form is from the Ohio River at Neville Island, Allegheny Co., which is 86 mm. in length. Individuals over 80 mm. in length are not rare in the larger rivers.

Colors (Plate A, Figs. 1 and 2). — The colors of this species are identical with those of C. propinquus. In fresh specimens the general ground color is light olive-green (Ridgway, 1886, X, 18), with darker spots in young specimens; in older individuals it is rather tawny-olive (III, 17). On the branchial region there is an oblique band of eream-eolor (VI, 20), edged by olive-green near the margin of the earapace, which is again cream-color. This cream-color in very brightly colored specimens sometimes becomes primrose-yellow (VI, 13). On the anterior margin of the carapace below the eyes there is a spot which may be rule (II, 7), ochraceous-rule (V, 5), edged with sulplur-yellow (VI, 14), ochre-yellow (V, 9), or primrose-yellow (VI, 13). The abdomen is olive-green or tawny-olive, shading into elestnut (IV, 9) on the anterior margins of the segments. There are one (sometimes two) median and two lateral rows of dark olive-green patches. The chelæ are light olive-green, shading distally into olive-yellow (VI, 16). The finger-tips are orange-buff (VI, 22), orange (VI, 3), or raw sienna (V, 2), followed by a pale, and a dark green, sometimes almost black band. The latter is not always present. The upper surface of the hand at the base of the daetylopodite has two (rarely one) rufous or ochraceous-rufous (V, 5) articular tubercles. The tubercles of the hand are *buff-yellow* (VI, 19) or *buff* (V, 13). The articular membranes of the hand are wine-purple (VIII, 15). The legs are olive-yellow (VI, 16) and whitish, with *olive-green* on upper edges.

The above colors fade in old specimens, and are often obscured by blackish or brownish coats of dirt. A variety with the chelæ and anterior parts of the carapace of a pale dirty bluish color was repeatedly observed in the Alleghany River at Sandy Creek and Twelve Mile Island, but only old specimens of this form were found. Young specimens generally vary more toward green, old ones toward tawny or brown.

The color of the newly laid eggs ranges from sage-green (X, 15) to dark olivegreen (X, 18), or often to almost black. When somewhat advanced in development, the egg becomes in part *prune-purple* (VIII, 1), in part *cream-color* (VI, 20), or whitish.

Of this species, seven hundred and twenty-one specimens are at hand. Most of them (six hundred and sixty-two) are from the state of Pennsylvania; fifty-seven are from the "Panhandle" of West Virginia, and two from Maryland (Wills Creek, Ellerslie). Many others have been collected, but no record has been kept, since they were used for exchange, dissection, and experiment.

DISTRIBUTION.

(See Plate XLII, Figs. 2 and 3.)

LOCALITIES REPRESENTED IN THE COLLECTIONS OF THE CARNEGIE MUSEUM.

PENNSYLVANIA: Greene County, Pennsylvania Fork of Fish Creek, Deep Valley; Smith Creek, Waynesburg; Bates Fork, Deer Lick; Pumpkin Run, Rice's Landing; Fayette County, Cheat River, Cheat Haven; Youghiogheny River, Connelsville; Washington County, Buffalo Creek, Taylorstown; Harmon's Creek, Dinsmore; Raccoon Creek, Burgettstown; Pigeon Creek and Taylor's Run, Monongehela City; Beaver County, Beaver (S. N. Rhoads coll.); Raccoon Creek (Atkinson, Williamson and Todd coll.); Little Beaver Creek, New Galilee (A. Kœnig coll.); Brady's Run, Fallston; Ohio River, Baden; Ohio River, Ambridge; Lawrence County, Eckles Run, Wampum; Big Run, Newcastle (D. C. Hughes coll.); Mercer County, Otter Creek, Mercer; Shenango Creek, Hadley (O. E. Jennings coll.); Crawford County, Shenango River, Linesville; Shermansville (O. E. Jennings coll.); Conneaut Outlet (D. C. Hughes coll.); Oil Creek, Spartansburg; Erie County, Conneaut Creek, Albion; Elk Creek, Miles Grove; French Creek, Union City; Butler County, Tributary of Slippery Rock Creek, Branchton; Thorn Creek, Renfrew; Rough Run, West Winfield; Allegheny County, Ohio River, Neville Island; Ohio River, Bellevue (E. Hays and R. Taylor coll.); Ohio River, Shoustown; Flaugherty Run, Moon Township (Q. T. Shafer coll.); Chartiers Creek, Carnegie (D. A. Atkinson coll.); Chartiers Creek, Bridgeville (D. A. Atkinson coll.); Turtle Creek, Pitcairn (D. A. Atkinson coll.); Youghiogheny River, Boston (D. A. Atkinson coll.); Crystal Lake, Pittsburgh (D. A. Atkinson coll.); Girty's Run, Millvalc; Stone Run, Thornhill; Pine Creek, below Bakerstown Station (D. A. Atkinson coll.); Alleghany River, Six Mile Island, (S. N. Rhoads and E. B. Williamson coll.); Squaw Run, Aspinwall; Alleghany River, Sandy Creek; Alleghany River, Verona (D. A. Atkinson coll.); Alleghany River, Twelve Milc Island; Deer Creek, Harmarville; Little Deer Crcek, Russelton; Pucketta Creek (D. A. Atkinson coll.); Little

Bull Creek, Tarentum (A. Kœnig coll.); Alleghany River, Butler Junction; Westmoreland County, Kiskiminetas River, Livermore; Conemaugh River, Blairsville Intersection; Reservoir of McGee Run, Derry; Whitethorn Creek, Dundale; small tributary of Loyalhanna River, New Alexandria; Loyalhanna River, Ligonier; Loyalhanna River, Crisp; Indiana County, Two Lick and Yellow Creeks, Homer; Crooked Creek, Creekside; Little Mahoning Creek, Goodville; Armstrong County, Long Run, Avonmore Station; Alleghany River, Kittanning; Alleghany River and Pine Creek, Mosgrove; Alleghany River, Templeton; Clarion County, Alleghany River, Red Bank; Jefferson County, Pond at Punxsutawney; Clearfield County, Sandy Lick Creek, Du Bois; Venango County, Alleghany River, Franklin; Oil Creek, Oil City; Forest County, Alleghany River, Tionesta; Warren County, Brokenstraw Creek and Crouse Run, Garland; McKean County, Alleghany River, Larabee; Bedford County, Wills Creek, Hyndman.

WEST VIRGINIA: Hancoek County, Harmon's Creek, Holidays Cove; Brooke County, Harmon's Creek, Colliers; Ohio County, Wheeling Creek, Elm Grove; Marshall County, Wheeling Creek, Union Township; Grave Creek, Cameron; Pennsylvania Fork of Fish Creek, Nuss; Wetzel County, Fishing Creek, New Martinsville.

MARYLAND: Alleghany County, Wills Creek, Ellerslie.

PREVIOUS RECORDS.

Type locality : New York, Monroe County, Genessee River, Rochester (Hagen), New York : *Cattaraugus County*, Alleghany River, Salamanca (Ortmann).

PENNSYLVANIA: Westmoreland County (Faxon); Allegheny County (Williamson); Warren County, Alleghany River, Corydon (Ortmann).

ADDITIONAL LOCALITIES.

Material in the Department of Agriculture, Harrisburg, collected by W. R. McConnell. — Shenango River, Jamestown, Mercer County; French Creek, Franklin, Venango County; small stream and pond, below Indiana, Indiana County; Branch of Genessee River, Ulysses, Potter County.

Alleghany River, Montrose, Allegheny County, Pa. (collected by the writer, but material used for study); Indian Creek, Jones Mills, Westmoreland County, Pa., (seen by the writer);¹⁴ Harmon's Creek, Hanlan, Washington County, Pa. (seen by the writer); Ohio River, Congo, Hancock County, W. Va., (seen by the writer).

¹⁴This locality was discovered in the beginning of the investigation by the writer, and since its importance was then not understood, no specimens were preserved; but the record is absolutely trustworthy.

REMARKS.

Cambarus obscurus is the river species of the Upper Ohio drainage. It is widely distributed in western Pennsylvania. Compared with the allied species *C. propinquus*, which occupies a much wider area, it is rather uniform in its characters all over its known range. It nowhere reveals a tendency to vary in the direction of *C. propinquus*, or of *propinquus sanborni*. This is the more remarkable because *C. propinquus* distinctly inclines toward this species in Erie and Crawford Counties, (in the lake drainage), and likewise because *C. propinquus sanborni* shows such a tendency in Wetzel County, West Virginia.

The variations observed in our abundant material have been briefly indicated above. However, it deserves special mention that the specific characters are scarcely subject to any variation.

Very interesting conditions are offered by the spines of the outer lower margin of the meropodite of the eheliped. One or two spines may be present, the proximal one smaller and often represented only by a small tubercle. Looking over ourmaterial, I find that only one spine is present in all individuals from the upper Alleghany drainage, including all the tributaries from Red Bank Creek northward (sixty-one specimens are at hand). In Armstrong, Indiana, Westmoreland, and Allegheny Counties, in the drainage of the Alleghany River, and in the whole drainage of the Monongahela, the Beaver, and Oliio proper, a second spine may be present, but such eases are not frequent, and generally this spine is found only on one of the two chelipeds. There is a tendency of this character, more frequently displayed in the southwestern extremity of the range. Two such spines on either side (right and left) are very rare, and I have found them only in twenty speeimens; fifteen of which belong to the Ohio drainage: two to that of the Monongahela, six to that of the Beaver, and seven to that of the Ohio below Beaver. Two eases were discovered in Wills Creek, Maryland, and three in Conneaut Creek at Albion, Erie County, Pa.

The latter specimens are interesting inasmuch as in Erie and Crawford Counties two drainage areas come together with that of Lake Erie, namely, that of the Shenango River, a tributary of the Beaver, and that of French Creek, a tributary of the Alleghany. In the latter creek and its tributaries I have never seen an individual with two spines (seventeen specimens are at hand). Among the material from the Beaver River drainage (fifty-six specimens) there are twentyone with two spines. Thus the tendency to develop two spines is markedly present in the drainage of the Beaver, while it is apparently absent in French Creek.

The specimens from the Lake Erie drainage in Conneaut Creek quite often have two spines (eight specimens out of twenty-two), and thus correspond to the Beaver River form, and to those from Elk Creek, in which one specimen out of six has two spines. Thus it appears that the form in the drainage of Lake Erie more closely approaches the form found in the Beaver River than that found in French Creek, although it must be granted that the material at hand seems to be not entirely satisfactory, being somewhat too scanty from French Creek, and decidedly insufficient from Elk Creek.

A few freaks have come under observation in the following eases :

1. As has been said, the rostrum reveals in old individuals a tendeney to a shortening of the aeumen. The extreme is reached in a specimen (male of the first form) 74 mm. long, from Conneaut Outlet, Crawford County (D. C. Hughes coll.), where the aeumen is broadly triangular and hardly longer than the short marginal spines, reaching only to the distal end of the basal joint of the pedunele of the antennula. The acumen is well formed (not deformed), showing no traces of injury. But that this specimen undoubtedly has been injured at some time earlier in its life, is revealed by the fact that both elaws are comparatively small, and by the characters of regeneration (lack of spines on the outer lower margin of the meropodite, the absence of a tuberele on the anterior margin of the lower side of the earpopodite, and the generally weak and slender shape).

2. A female (46 mm. long) from Brokenstraw Creek, Garland, Warren County, has the aeumen of the rostrum directed obliquely to the left side, and the right margin of the rostrum has five marginal spines. This seems to be due to an injury received in earlier life. The left elaw is also smaller and of the regenerated type.

3. A specimen (55 mm. long) from the Alleghany River at Sandy Creek (eollected by the writer, Nov. 19, 1904, Cat. No. 74, 479), has the characters of a female in the shape of the chelæ and the laek of hooks on the pereiopods. The annulus ventralis, however, is very indistinct, although its outlines and slight median depression are visible, as is also the median fissure. But this individual has the male genital opening in the coxopodite of the fifth pereiopod, and the first pleopod is of the male type, although small; it is unusually short, reaching only to the anterior margin of the coxopodites of the fourth pereiopods; it is of the type of the first form, with a distinct shoulder; the outer part is horny and distinctly longer than the inner part. The second pleopods are entirely of the male type. According to the sexual orifice and the copulatory organs, we are to regard this as a male with certain female characters.

4. A pendant to the last specimen is one (67 mm. long) from the Ohio River,

Neville Island, (collected by D. A. Atkinson, May 14, 1899, Cat. No. 74. 36). The claws are intermediate between male and female, but inclining toward the male form. The third pereiopods have strong and well developed hooks on the ischiopodites of the type of the first form male. The first pleopods are very peculiar, (Plate XXXIX, Figs. 7d and 7e), and unlike those of C. obscurus; they rather resemble those of C. limosus. Their length and strength are normal, but there is no shoulder, and the two parts are separated only for a short distance at the tips, similar to C. limosus, but the tips are not twisted. The outer tip is horny and pointed, the inner soft, thicker, and tapers to a blunt point. The second pleopods are of the normal male type. In addition this individual possesses a well developed annulus ventralis, and sexual orifices only on the third pereiopods. Thus it appears to be a female, with the secondary sexual characters of the male well, but not specifically, developed.

None of the two cases of apparent hermaphroditism just described (Nos. 3 and 4) agrees with any of the four cases mentioned by Faxon, (1885*a* p. 13, 14), or the four described by Hay, (1905, p. 226 and 227). Additional cases will be described below under *C. bartoni*. There is in the Carnegie Museum a further individual of hermaphroditic character, namely a specimen of *Cambarus rusticus* Girard, from the Wabash River, Bluffton, Indiana, collected by Mr. E. B. Williamson, June 1, 1905, Cat. No. 74, 578. I append a description of it.

The specimen is externally a female, possessing the female type of claws, a welldeveloped annulus, female sexual openings, and no hooks on the third pereiopods. But the first pleopods are peculiar; they are short and stout; the bases are identical with those of the male pleopods; the distal parts, however, reach only to about the middle of the coxopodites of the fourth pereiopods; their tips are soft, blunt, and slightly curved inward, and possess the furrow which divides them into an outer and inner part, but these parts are not separated at the tips. The second pleopods are of the female type. This case corresponds in a certain degree to the second, third, and fourth, mentioned by Faxon, chiefly so to the third (in *C. diogenes*). The specimen is apparently a normal female, only the first pleopods are transformed in a peculiar way, resembling the male type generally, but differing from the specific shape. In the present case the first pleopod is different from Faxon's case in detail.

4. CAMBARUS (BARTONIUS) BARTONI (Fabricius).

Plate B, Fig. 1; Plate XXXIX, Fig. 1a-1f, and Fig. 8; Plate XL, Fig. 2.)

Astacus bartoni Fabricius, 1798, p. 407; Say, 1817, p. 167; Harlan, 1835, p. 230, f. 3; Gould, 1841, p. 330; Thompson, 1842, p. 170; De Kay, 1844, p. 22, Pl. 8, f. 25; Gibbes, 1850, p. 195, (partim).

Astacus ciliaris Rafinesque, 1817 p. 42.

Astacus pusillus Rafinesque, 1817, p. 42.

Astacus affinis Milne-Edwards, 1837, p. 332 (non Say).

Cambarus bartoni Girard, 1852, p. 88; Bell, 1859, p. 210; Hagen, 1870, p. 75, Pl. 1, f. 47-50, Pl. 2, f. 135-139, Pl. 3, f. 166; Abbott, 1873, p. 80; Smith, 1874, p. 639; Putnam, 1874, p. 191; Faxon, 1884b, p. 22; Faxon, 1885a, p. 59; Faxon, 1885b, p. 358; Underwood, 1886, p. 367; Ganong, 1887, p. 74; Faxon, 1890, p. 622; Hay, 1896, p. 487, f. 6; Faxon, 1898, p. 649; Osburn and Williamson, 1898, p. 21; Williamson, 1899, p. 47; Hay, 1899, p. 959, 966; Williamson, 1901, p. 11; Ortmann, 1905a, p. 390; Paulmier, 1805, p. 134, f. 6; Rathbun, 1905, p. 18.
Cambarus pusillus and montanus Girard, 1852, p. 88.

Cambarus (Bartonius) bartoni Ortmann, 1905b, p. 120, 134.

Body robust, very sparsely pubescent in fresh, but perfectly naked in old specimens, with only a few hairs on the fingers of the chelæ, and sometimes a slight pubescence on the cutting edge of the fingers.

Carapace subovate, strongly depressed. G: H: B = 1: 1.3 or 1.4: 1.5 or 1.6. Greatest width of branchial regions well forward, at a short distance behind the cervical groove. Upper surface of carapace very flat.

Cervical groove deep, not interrupted on the sides. Areola distinctly longer than half of the anterior section of carapace; a:p = 1:0.6 Areola rather broad (w:l = 1:5 or 6), with about 3-5 irregular rows of punctures.

Rostrum (Plate XXXIX, Fig. 1a-1f) broad and short, reaching generally to the distal end of the second joint of the peduncle of the antennula, and hardly beyond the middle of the fourth joint of the peduncle of the antenna. Upper surface almost flat or only slightly concave, but margins elevated, without marginal spines. The margins converge more or less from the base, sometimes they are almost parallel, and near the apex they are suddenly contracted into a short, triangular acumen having a sharp point. The angles at the base of the acumen are rounded, but generally well marked, and the elevated margins are continued to the apex, although slightly decreasing distally from the lateral angles. Postorbital ridges short, almost parallel, angulated anteriorly, but without spine, except in young specimens.

Surface of carapace, punctate, distinctly granulated on the hepatic region in larger specimens. There are also a few more or less distinct granulations immediately behind the cervical groove, but no spine. External orbital angle well marked by an angulation or a small tubercle, more rarely, and only in young specimens, spiniform. Branchiostegal spine formed by a small tubercle, which is sometimes obsolete.

Abdomen as long as carapace, or slightly shorter or longer; it is slightly wider in the female than in the male, but hardly wider than the carapace in the former. Anterior section of telson on the posterior lateral corners generally with two, more rarely with three spines. Posterior section semi-elliptical, distinctly wider than long, slightly shorter than anterior section.

Epistoma with posterior part broad and short, about two and a half times as broad as long, with a distinct transverse groove on either side slightly posterior to the middle, and an anterior median depression. Anterior section constricted at the base, semi-circular, with a median anterior point. This point may be strongly developed, or almost entirely absent. Transverse diameter distinctly greater than the longitudinal.

Antennula with a small, often spiniform, tubercle on the lower margin of the basal joint.

Antennal peduncle with a tubercle on the outer side of the first joint, which is often spiniform, chiefly so in young specimens; second joint with or without a very indistinct tubercle.

Antennal scale short and narrow, slightly longer than the rostrum, reaching to, or almost to, the end of the fourth joint of the antennal peduncle. Spine of outer margin strong. Laminar part not much broader than the marginal spine.

Flagellum reaching to the anterior margin or to the middle of the telson in the male, slightly shorter in the female, but sometimes considerably shorter, without apparent trace of having been injured. In some cases it reaches only the middle of the second abdominal segment.

First pereiopods (Plate XL, Fig. 2) very strong and robust in old individuals, particularly males. Hand elongate-ovate, broad, and strongly depressed. Surface punctate. Inner margin of palm short, curved, with a single marginal row of more or less distinct, low tubercles. Outer margin smooth, rounded proximally, carinate distally. Fingers longer than palm, not gaping in young individuals, but with a wide gap at the base, meeting only at the tips, most noticeably in old males. Outer margin of movable finger punctate, or, in older specimens, with a few indistinct tubercles. Cutting edges with tubercles, larger in the proximal part. Upper surface of each finger with a low longitudinal rib, bordered by rows of punctures. This rib often becomes indistinct, especially on the movable finger in old males.

Carpopodite slightly longer than wide, shorter than palm, with a deep longitudinal sulcus above. Inner margin with a strong pointed or blunt spine, which is generally distinctly hooked, going off almost at a right angle, but curving forward in the distal part. A small spine or tubercle (sometimes double) may be added to
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it proximally. Lower surface with a blunt conical tubercle in the middle of the anterior margin (occasionally spiniform). The tubercle at the articulation with the hand is generally obsolete. There are sometimes additional tubercles; the one which most frequently occurs is a small spine or tubercle between the large one on the inner margin and that on the anterior margin of the lower side.

Meropodite smooth, with 1-3 tubercles near the distal end of the upper margin, one of which is often spiniform in young specimens; in old specimens they are generally very indistinct or wanting. Lower side with two rows of spiniform tubercles. The outer rows consist of 1-6 (very rarely only one tubercle). Six were found in only one instance, that of a regenerated cheliped. Generally there are two or three. The inner row has 6-11 spiniform tubercles, of which the distal is the largest. A small tubercle on the outer articulation with the carpopodite may be present or absent.

Ischiopodite of third pereiopod hooked in the male. The hook of the first form is strong and subconical.

The *coxopodite* of the fourth pereiopod in the male possesses a prominent rounded and compressed tubercle.

First pleopods of the male of the first form (Plate XXXIX, Fig. 8) stout and short, reaching to the posterior margin of the coxopodite of the third pereiopods. They are not articulated at the base. The two parts are separated at the tips for a short distance, and both are curved sharply backward, forming almost a right angle with the basal part. Distally they are partly twisted, so that the outer part is directly anterior to the inner. The outer part is horny, compressed, falciform, the tip pointed, with a small posterior accessory point (often worn off). The inner part is soft, swollen at the base, and suddenly tapering to a blunt point.

In the male of the second form this organ may be articulated at the base (in the case of the young) or not articulated (in older specimens). Both parts are separated distally for a short distance, and the outer part is soft, not horny, less distinctly compressed, and blunt. In the young these organs are considerably shorter than in older specimens.

Annulus ventralis of the female transversely rhombiform, with a deep central depression and a longitudinal S-shaped fissure. Anterior and more particularly the posterior margins elevated. The whole anterior portion of the annulus often appears depressed compared with the elevated posterior margin. Where the longitudinal fissure passes over the posterior margin the latter is slightly depressed. In young females the central depression is less marked, and the margins are consequently less elevated, giving a rather flat appearance on the annulus.

Size. — This species in western Pennsylvania reaches a considerable size, although the maximum recorded by Hagen (3.6 = 91 mm.) has not been observed. Faxon, (1885*a*, p. 64), mentions a specimen from the Mammoth Cave, Ky., measuring 108 mm., but this is not the typical form. The largest individuals in the Carnegie Museum are two females, the one from Braeburn, the other from Derry, Westmoreland County, both measuring 87 mm. in length. The largest male (first form) is from North Versailles Township, Allegheny County, and measures 83.5 mm.¹⁵ In western Pennsylvania specimens over 80 mm. are not altogether rare.

In the eastern portions of the state this species is much smaller. The largest specimen at hand is a female from Roxboro, 67 mm. long, and a male (first form) from Manayunk, Philadelphia County, 66.5 mm. long, (both collected by H. Gera). Specimens over 60 mm. are not frequent in eastern Pennsylvania.

Colors. — Generally dull and not much varied, greener in young specimens, browner in old ones. (See Plate B, Fig. 1.)

The carapace and abdomen *olive-green* (Ridgway, 1886, X, 18) to *tawny-olive* (III, 17), *chestnut* (IV, 9), and *burnt umber* (III, 8), a shade darker dorsally, lighter on the sides. Margins of rostrum, in the browner specimens, *ferrugineous* (IV, 10). Distal third of finger *rufous* (IV, 7), or *tawny* (V, 1). Tubercles of the cutting edges of fingers *ochraceous buff* (V, 10). In brown individuals there is generally some green on the chelæ.

Aside from young individuals, where the normal olive-green prevails, this species shows a distinct tendency toward the brown and chestnut shades, more so than the river species, *C. limosus*, *C. propinquus*, and *C. obscurus*.

In some cases the colors are brighter. Individuals shading to a copper-color are not rare, and I have seen a few where a dirty slate-blue was the ground-color. Of course, as in other species, in old specimens the original colors are largely obscured by a deposit of mud, rendering the specimens sometimes almost black.

In very young specimens (10 to 20 mm. long) the color is olive-green, semitransparent, with the chelæ almost entirely ferrugineous.

The color of the newly laid eggs is almost black, with, or without, a purplish hue (*indian-purple*, VIII, 6). In a more advanced stage they become particolored: *prune-purple* (VIII, 1) or *dahlia-purple* (VIII, 2) on one side, *grayish* or *whitish* on the other.

The Carnegie Museum possesses seven hundred and fifty-five specimens of this species, six hundred and fourteen of which are from the state of Pennsylvania,

¹⁵ The female from Hill, Westmoreland County, mentioned previously (Ortmann, 1905*a*, p. 391) is 85 mm., not 89 mm. as stated ; the male from Cheat River (*ibid.*) is not 92 mm., but 82 mm. in length.

nineteen from New York, ten from New Jersey, six from Ohio, seventy from West Virginia, thirty-four from Maryland, and three from North Carolina.

DISTRIBUTION.

Localities represented in the collection of the Carnegie Museum.

PENNSYLVANIA: Delaware County, Dicks Run, Wallingford; Philadelphia County, Manayunk, (H. Gera coll.); Domino Lane Run, Roxboro, (H. Gera coll.); Wissahickon; Bucks County, Grenoble; Dark Hollow Run, New Hope; Northampton County, Bushkill Creek, Easton, (A. E. Davison coll.); Lehigh County, Little Lehigh Creek, Emaus; Montgomery County, West Manayunk, (H. Gera coll.); Bucks County, Shoemakersville; Chester County, Valley Forge; Lancaster County, Pequea; York County, Arthur Run, York Furnace; Dauphin County, Susquehanna River, Halifax; Northumberland County, Georgetown; Franklin County, Diekey; Williamson; Fulton County, Dogtown; Big Cove Creek, McConnellsburg; Blair County, Frankstown Branch of Juniata River, Loop near Hollidaysburg; Bedford County, Bedford Springs (A. Koenig coll.); Cameron County, Sinnamahoning Creek, Driftwood; Sinnamahoning; Cambria County, Tributary of Clearfield Creek, Ashville; Headwaters of Clearfield Creek, Cresson; Summit, (S. N. Rhoads coll.); Laurel Run, Lovett; Somerset County, Wills Creek, Manee; Flaugherty Creek and tributaries, Sandpatch; Casselman River, Rockwood; Windber; Laurel Hill, west of Jennerstown; Indiana County, Cush-Cushion Creek, west of Cherry Tree; Homer; Creekside; Goodville; Jefferson County, Mahoning Creek, Punxsutawney; Brockwayville; Brookville; Clearfield County, Falls Creek; Elk County, Elk Creek, Ridgway; Potter County, Keating Summit; McKean County, Larabee; Warren County, Crouse Run, Garland; Forest County, Tionesta; Venango County, Sage Run, Oil City; Clarion County, Alleghany River, Red Bank; Armstrong County, Long Run, Avonmore Station; Weskit, opposite Kittanning; Pine Creek, Mosgrove; Alleghany River, Templeton; Westmoreland County, Tub Mill Run, Ross Furnace, South of New Florence; Crisp (H. H. Smith and M. A. Wertheimer coll.); Lynn's Run, Mechanicsburg; Loyalhanna River, Ligonier; Indian Creek, Jones Mills; Reservoir of McGee Run, Derry; Withethorn Creek, Dundale; Livermore; Hill, opposite Leechburg; Braeburn; Fayette County, Youghiogheny River, Ohiopyle; Jaeobs Creek, Laurelville; Dunbar; Cheat Haven; Allegheny County, Alleghany River, Butler Junetion; Little Bull Creek, Tarentum, (A. Koenig eoll.); Deer Creek, Harmarville; Little Deer Creek, Russelton; Power's Run, Montrose; Squaw Run, Aspinwall; Verona, (D. A. Atkinson eoll.); Quigley's Run, Verona; Breakneck Run, Bakerstown Station; Pine Creek, below Bakerstown Station, (D. A. Atkinson coll.); Stone Run, Thornhill;

Girty's Run, Millvale; Westview (D. A. Atkinson coll.); Avalon; Edgeworth, (G. H. Clapp coll.); Schenley Park, Pittsburgh, (E. B. Williamson coll.); Fern Hollow, Pittsburgh; Edgewood Park, Swissvale; North Versailles Township, opposite Stewart; Jacks Run, South Versailles Township; Boston, (D. A. Atkinson coll.); Thompson's Run, Kennywood, (F. E. Kelly coll.); Carnegie, (D. A. Atkinson coll.); Moon Township, (D. A. Atkinson, B. Graf, E. B. Williamson, A. T. Shafer, Q. T. Shafer coll.); Thorn's Run, Moon Township; Flaugherty Run, Moon Township, (Q. T. Shafer coll.); Butler County, West Winfield; Renfrew; Slippery Rock Creek, Branchton; Erie County, Elk Creek, Girard; Walnut Creek, Swanville; Crawford County, Spartansburg; Linesville; Mercer County, Stoneboro, (D. A. Atkinson); Mercer; Lawrence County, Wampum; Big Run, Newcastle (D. C. Hughes coll); Beaver County, Ambridge; Baden; Beaver, (S. N. Rhoads coll.); Brady's Run, Fallston; Smith's Ferry; Monaca; Washington County, Monongahela City; West Brownsville; Francis Mine, near Burgettstown; Taylorstown; Greene County, Rice's Landing; Bates Fork, Deer Lick; Waynesburg; Deep Valley.

NEW YORK: *Herkimer County*, East Canada Creck, Dolgeville, (R. Ruedemann coll.).

NEW JERSEY: Mercer County, Princeton.

MARYLAND: Washington County, Home's Valley, (F. Silvester coll.); Alleghany County, South Cumberland; Corriganville; Rawlings; Garret County, Selbysport; Stoyer.

WEST VIRGINIA: Morgan County, Cherry Run; Tucker County, Blackwater River, Davis; Shavers Fork, Parsons; Monongalia County, Cheat River, (H. H. Smith coll.); Morgantown; Pleasants County, St. Mary's; Wetzel County, New Martinsville; Marshall County, Cameron; Ohio County, Elm Grove; Brooke County, Colliers; Hancock County, Holidays Cove; Congo.

OHIO: Harrison County, Bowerstown; Carroll County, New Hagerstown.

NORTH COROLINA: Watauga County, Blowing Rock, (Wilcox coll., Exch. Acad. Nat. Sc. Philad.).

PREVIOUS RECORDS.

Type Locality : North America, (Fabricius); Philadelphia, Pa., (Harlan).

CANADA: Falls of Ouiatchouan, Lake St. John, Quebec, (Bell); Metis and Matapediac Rivers, Quebec, (Bell); Montreal, Quebec, (Faxon); Restigouche River, New Brunswick, (Bell); Upsalquitch River, New Brunswick, (Ganong); Miramichi River. New Brunswick, (Ganong); St. John, New Brunswick, (Faxon); St. John River, Grand Falls to Fredericton, New Brunswick, (Ganong).

MAINE: Houlton and Maysville, Aroostock County, (Faxon); Outlet of Moosehead Lake, Piscataquis County, (Faxon); Madison, Somerset County, (Faxon).

VERMONT: (Thompson); Burlington, Colchester, and Shelburne, Chittenden County, (Faxon).

MASSACHUSETTS: (Gould); Williamstown, Berkshire County, (Faxon); North Adams, Berkshire County, (Faxon); North Crafton, Worcester County, (Faxon).

NEW YORK: Lake Champlain, (Rafinesque); Ellenburg, Clinton County, (Faxon); Elizabethtown, Essex County, (Hagen); Westport, Essex County, (Faxon); Lake George, Warren County, (Rafinesque); Saratoga County, (Rafinesque); Fishkill, Dutchess County, (Rafinesque); Newburgh, Orange County, (Rafinesque); Port Jervis, Orange County, (Faxon); New York City, (Paulmier); Fallsburg, Sullivan County, (Faxon); Fulton Lakes, Hamilton and Herkimer Counties, (Faxon); Canton, St. Lawrence County, (Faxon); Utica, Oneida County, (Rafinesque); Oswego, Oswego County, (Rafinesque); Cazenovia, Madison County, (Faxon); Sherburne, Chenango County, (Faxon); Berkshire, Tioga County, (Hagen); Ithaca, Tompkins County, (Faxon); Rochester, Monroe County, (Faxon); Niagara, Niagara County, (Hagen); Forestville, Chautauqua County, (Faxon).

NEW JERSEY: Schooley's Mountain, Morris County, (Hagen); Orange, Essex County, (Faxon); Trenton, Mercer County, (Abbott); Princeton, Mercer County (Ortmann).

PENNSYLVANIA: Windham, Bradford County, (Faxon); Headwaters of Loyalsock Creek, Sullivan County, (Ortmann); Ganoga Lake, Sullivan County, (Ortmann); Berwick, Columbia County, (Girard); Schuylkill River, Philadelphia, (Hagen); Chester County, (Faxon); Bainbridge, Lancaster County, (Faxon); Hummelstown, Dauphin County, (Faxon); Carlisle, Cumberland County, (Girard); Pinegrove, Cumberland County, (Ortmann); McKean County, (Faxon); Foxburg, Clarion County, (Girard); Westmoreland County, (Faxon); Pittsburgh, Allegheny County, (Williamson); Bedford and Loysburg,¹⁶ Bedford County, (Faxon).

DELAWARE: Greenville, New Castle County, (Ortmann).

MARYLAND: Harford County, (Faxon); Howard County, (Faxon); Montgomery County, (Faxon); Frederick County, (Faxon); Washington County, (Faxon); Cumberland, Alleghany County, (Girard); Garrett County, (Faxon).

DISTRICT OF COLUMBIA: Georgetown, (Hagen); Washington, (Faxon).

VIRGINIA: Alexandria County, (Faxon); Clarke County, (Faxon); Stafford County, (Faxon); James River, (Faxon); Franklin, Southampton County, (Faxon); Lunenburg, Lunenburg County, (Faxon); Waynesboro, Augusta County, (Faxon);

¹⁶ Faxon cites "Pattonville, Bedford County." The name of Pattonville has been changed to Loysburg, which the bamlet originally bore. It is situated in the valley known as Morrison's Cove, a beautiful spot full of clear mountain streams, formerly abounding in brook-trout. The locality must not be confounded with Pattonville in Delaware County, (P. O. Fernwood).

Rockbridge County, (Girard); Bath County, (Faxon); Pulaski, Pulaski County, (Faxon); Wytheville, Wythe County, (Faxon); Smith County, (Faxon).

NORTH CAROLINA: Kinston, Lenoir County, (Faxon); Newman's Fork, Blue Ridge, McDowell County, (Faxon); Black Mountain, McDowell County, (Faxon); Waynesville, Haywood County, (Faxon); Roan Mountain, 6,000 feet, (Faxon).

TENNESSEE: Doe River, Carter County, (Faxon); Claiborne County, (Faxon); Monroe County, (Faxon); McMinn County, (Faxon).

KENTUCKY: Kentucky River, Hickman's Landing, (Hagen)¹⁷; Cumberland Gap, Bell County, (Faxon); Smoky Creek, Carter County, (Faxon); Little Hickman, Jessamine County, (Faxon); Albany, Clinton County, (Faxon); Grayson Springs, Grayson County, (Faxon); Mammoth Cave, Edmonson County, (Hagen).¹⁸

WEST VIRGINIA: Patterson Creek, (Faxon); South Branch of Potomac River, (Faxon); Williamsport, Grant County, (Faxon); Glade Creek, Randolph County, Faxon); Petroleum, Ritchie County, (Faxon).

Оню: Marietta, Washington County, (Faxon); Tuscarawas County, (Williamson); Knox County (Williamson); Licking County, (Williamson); Columbus, Franklin County, (Hagen); Alum Creek, and tributaries of Big Walnut and Big Darby, Franklin County, (Osborn and Williamson); Yellow Springs, Greene County, (Faxon); Warren County, (Faxon); Cincinnati, Hamilton County, (Hagen).

INDIANA¹⁹: New Albany, Floyd County, (Faxon); Cave near Paoli, Orange County, (Hay); Down's and Connelly's Cave, Lawrence County, (Hay); Bloomington, Monroe County, (Faxon); Clear Creek, Monroe County, (Hay); May's Cave, Monroe County, (Hay); Indianapolis, Marion County, (Faxon); Irvington, Marion County, (Hay).

The locality "Lake Superior" (Hagen) has been dropped, since it is, no doubt, erroneous, (see Ortmann, 1905, p. 135); the same is the case with "Osage River, Missouri" (Hagen).

ADDITIONAL NEW LOCALITIES.

NEW YORK: Altamont, Albany County, (N. Y. State Museum); Mill Creek, Wilmurt, Herkimer County, (N. Y. State Mus.); Spencerport, Monroe Co., (Mus. Oberlin).

PENNSYLVANIA:

Specimens preserved in the Academy of Natural Sciences of Philadelphia : 5717 Germantown Ave., Philadelphia ; small stream near Holmesburg, Philadelphia County;

¹⁷ Not located by writer.

¹⁸ The form from Mammoth Cave is not typical, according to Faxon and Hay.

¹⁹ Specimens from Indiana differ from the typical form, according to Faxon and Hay.

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Roberts Run, Abrams, Montgomery County; Port Alleghany, McKean County; Corydon, Warren County.

Specimens preserved in the Department of Agriculture, Harrisburg: Buckingham, Bucks County; Avondale, Chester County; Highspire, Dauphin County; Harrisburg, Dauphin County; Rockville, Dauphin County; Dauphin, Dauphin County; Marshrun, Perry County; Gettysburg, Adams County; Montalto, Franklin County; Emmaville, Fulton County; Huntingdon, Huntingdon County; Williamsport, Lycoming County; New Albany, Bradford County; Wellsboro, Tioga County.

Mr. W. R. McConnell collected this species at the following localities : Stream flowing out of Beach Lake, Wayne County; small stream tributary to Delaware River, Portland, Northampton County; stream flowing into Lehigh River, Slatington, Lehigh County; Schuylkill River, Reading, Berks County; Toby's Creek, Kingston, Luzerne County; Fish Creek, near Stillwater "fifteen miles above Bloomsburg," Columbia County; Montour Run, Greenpark, Perry County; Big Buffalo Creek, Erly, Perry County; Conococheague Creek, Chambersburg and Marion, Franklin County; tributary of Conococheague Creek, Mercersburg, Franklin County; Laurel Run and Shafer's Run (probably Shaver's Creek, both in northeastern part of county), Huntingdon County; Slab Cabin Creek and Thompson's Spring, State College, Center County; Bear Meadows and branch of Spring Creek, Boalsburg, Center County; Sinking Creck, Center Hall, Center County; Bald Eagle Creek and Wallis Run, Milesburg, Center County; Beech Crcek, Beech Creek Station, Clinton County; Fishing Creek and tributary, Lamar, Clinton County; Nipponose Creek, Jersey Shore, Lycoming County; branch of Genessee River, Ulysses, Potter County.

The writer has seen this species at and from the following localities :

Lafayette, Montgomery County, (H. Gera coll.); Leopard, Easttown Township, Chester County, (J. F. Sachse, Philadelphia, coll.); Wills Creek, Hyndman, Bedford County; Big Meadow Run, Ohiopyle, Fayette County; West Branch of Susquehanna, Cherry Tree, Cambria and Clearfield Counties.; Blairsville Intersection, Westmoreland County; Springs on Chestnut Ridge, near Derry, Westmoreland County, elevation 1800 fcet; Coalpit Run, Millbank, Westmoreland County; Donegal, Westmoreland County; Jeanette, Westmoreland County; Alleghany River, Hulton, Allegheny County; tributary of Thompson's Run, south of North Bessemer, Allegheny County; Sandy Creek and Alleghany River, Sandy Creek, Allegheny County; Nine Mile Run, Pittsburgh, Allegheny County; Dinsmore, Washington County; Summit and Conncautville Station, Crawford County.

MARYLAND: Sideling Creek, Washington County, (H. A. Pilsbry coll., Acad.

Nat. Sc. Phil.); Town Creek, Alleghany County, (H. A. Pilsbry coll., Acad. Nat-Sc. Phil.); Deer Park, Garrett County, (P. R. Uhler coll.). (See below under *C. diogenes*, footnote 26.)

REMARKS:

Cambarus bartoni is the crawfish of the small streams in Pennsylvania, and is exceedingly abundant all over the state.

In spite of its wide distribution over parts considerably different in physical conditions, this species is in Pennsylvania very uniform with regard to its morphological characters (disregarding the variety *robustus*, to be discussed below). It is true that in the foregoing description many characters are pointed out which vary within certain limits; but these variations are not restricted to certain parts of the state, but occur everywhere. It is even hard to say of any character that it prevails in a certain region. In general there are indications that the species is more flourishing and also more variable in the western part of the state than in the eastern. This observation, however, applies chiefly to characters which appear in very old specimens, as for instance, a stronger development of the tubercles on the inner margin of the hand and on the outer margin of the movable finger. Since the eastern form is much smaller, such characters, which are only occasionally present in very large specimens, are not found in specimens from the east, namely, strong sculpture of the hand and very thick margins on the rostrum.

The most variable feature of this species is the rostrum. Generally it is narrower and more gradually tapering in very young specimens (Pl. XXXIX, Fig. 1d and 1e). In older individuals it becomes broader, and is more suddenly constricted into a longer or shorter acumen. Beyond this there is no rule. The most frequent shapes are those figured on Pl. XXXIX, Fig. 1b and 1c. The one delineated in Fig. 1f is exceptional. The other extreme is shown in Fig. 1a, with margins practically parallel, and a very sudden constriction into a comparatively short and broad acumen. Although this last shape is more frequent in the western part of the state, it is also found in the extreme eastern portions of the commonwealth.

There is only one character in which regional variation may be observed, and this is the size of the body. As has been mentioned, in the eastern part of the state this species is considerably smaller than in the western, and the largest specimens are found west of the Chestnut Ridge. Individuals 80 mm. and more in length are not rare in Westmoreland, Allegheny, Elk, and Lawrence Counties. Specimens between 70 and 80 mm. long have been found, in addition to the counties just named, in Crawford, Venango, Potter, Jefferson, Butler, Armstrong, Washington, and

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Fayette. All of these are west of the Chestnut Ridge. East of the Chestnut Ridge, but west of the Alleghany Front, specimens over 80 mm. in length are rare; only one was found at Sand Patch, Somerset County, (86 mm. long). Specimens over 70 mm, in length are not infrequent here. In the Alleghany Mountain region, (between the Alleghany Front and the Blue Ridge) only a few instances of specimens over 70 mm, in length have been found, and none as large as 80 mm. The largest is from McConnelsburg, Fulton County, 77 mm. East of the Blue Ridge (South Mountain) the length 70 mm. is never attained. In the easternmost extremity of the state (Northampton and Bucks Counties) even the length of 60 mm. is not represented among my material, although I possess large series of specimens from this region. Thus it appears that the size gradually decreases from west to east. There is hardly any appreciable decrease in size from south to north. The smaller number of large individuals from the northwestern section of the state is very likely due to the fact that large collections were not made in that part of the state.

Freaks have been observed in several cases. Aberrant forms of the rostrum have been repeatedly found, and one variation has been encountered four times in which the rostrum has a very slightly developed acumen, so that it is almost evenly rounded off anteriorly, with only a small and indistinct median angle or point, (female, 25 mm., Schenley Park, Pittsburgh; femalc, 50 mm., Templeton, Armstrong County; male, first form, 64 mm., Branchton, Butler County; female, 80 mm., Monongahela City, Washington County). The rostrum, in these cases, is exceptionally short, due to a reduction of the acumen. A case of an unsymmetrical rostrum, with the left angle at the base of the acumen cut off, has also been observed; this is clearly a malformation due to some previous external injury.

We may class with the freaks a single specimen in which the carapace possesses a lateral spine. The specimen is a female (42 mm. long) from Weskit, Armstrong County, and it has a small, sharp, lateral spine, but only on the left side of the carapace. This is the more remarkable since it demonstrates the importance of this specific character. There is not a single other individual among the large material at hand which possesses such a spine, although granulations in its place arc not infrequent.

Two interesting cases of abnormally developed sexual characteristics have been noticed (compare the other cases mentioned under C. (Faxonius) obscurus).

1. A large female, 71 mm. long, found March 31, 1905, at Hollidays Cove, Hancock County, W. Va., (Cat. No. 74, 491), which is normal in every respect but one, and besides, is undoubtedly sexually normal, since it carried under the abdomen

ten young ones, ready to leave the mother, (very likely a number had left already when the mother was captured). It has on the ischiopodite of the left third pereiopod the copulatory hook of the male; this hook is not small or rudimentary, but strong, and similar to the hook as found in the male of the first form. The ischiopodite of the corresponding right pereiopod has no trace of this hook.

2. A specimen, 48 mm. long, was found in Fern Hollow, Pittsburgh, November, 22, 1905, (Cat. No. 74. 681), which externally (in the shape of the claws) looks like a female, but shows very indistinctly the sexual openings of the male, and no traces of those of the female. It also has the first pleopods of the male of the second form, but the second pleopods are built according to the female type. Further, it lacks entirely the hooks of the third pereiopods, and has a distinct female annulus, of juvenile type.

This case does not correspond exactly to any of those described previously. It resembles to a certain degree one of the cases in *C. obscurus* described above (No. 3), with the exception that here the first pleopods are of the type of the male of the second form, and that the second pleopods are not of the male, but of the female type.

4a. CAMBARUS (BARTONIUS) BARTONI ROBUSTUS (Girard).

(Plate B, Fig. 2. Plate XXXIX, Fig. 2a and 2b. Plate XL, Fig. 3.)

Cambarus robustus Girard, 1852, p. 90 ; Hagen, 1870, p. 80, Pl. 3, f. 167 ; Smith 1874, p. 639 ; Faxon, 1884b, p. 143.

Cambarus bartoni robustus Faxon 1885a, p. 61; Faxon, 1885b, p. 358; Underwood, 1886, p. 367; Faxon, 1890, p. 622; Faxon, 1898, p. 649; Osburn & Williamson, 1898, p. 21; Williamson, 1899, p. 20. 47; Hay, 1899, p. 959, 966; Williamson, 1901, p. 11; Ortmann, 1905a, p. 391; Ortmann, 1905b, p. 135.

Cambarus bartoni Williamson, 1905, p. 310.

The differential characters of this form are the following:

Body robust, attaining decidedly a more considerable size than the typical bartoni. The largest individuals at hand are a male, first form, from Spartansburg, Crawford County, measuring about 98 mm. (estimated, since rostrum is damaged); a female from Squaw Run, Allegheny County, measuring 94 mm. and a male, second form, from Puketta Creek, Allegheny County (A. Kœnig coll.), measuring 101 mm. I have quite a number of males (of the first and second form) and of females over 90 mm. long. It is also remarkable that specimens of this variety, of a considerable size (60 to 70 mm.) display characters which are distinctly juvenile, showing no tendency on the part of the chelæ to attain a large size. This tendency is also evidenced by the fact that the smallest males of the first form at hand are two individuals measuring 72 mm. (Union City and Hulton). From Oberlin, Ohio, I have seen a male of the first form, 71 mm. long, while the minimum size of sexually ripe males of the typical form is 50 mm. for western, and 49 mm. for eastern Pennsylvania.

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The shape of the carapaee is similar to that of *C. bartoni*, but, in old specimens, appears slightly more depressed on account of the wider hepatie and branchial regions; G: H: B = 1:1.3 to 1.5:1.5 to 1.7.

The rostrum (Plate XXXIX, Figs. 2a and 2b) is markedly different from the typical form, narrower, more tapering, and with a longer acumen; the upper surface is slightly concave. The shape is rather variable. In young specimens of the typical *C. bartoni* the rostrum often approaches the form of *C. bartoni* robustus, but on the other hand young specimens of the latter have a narrower rostrum than the former. (Compare Plate XXXIX, Fig. 1e and 2b). In many cases the rostrum of the variety is not longer than in the typical form, but in others it surpasses it, reaching to the middle, or even almost to the end of the third joint of the peduncle of the antennula, or to the base or almost to the middle of the fifth joint of the peduncle of the antenna.

Areola similar to that of the typical form, but with a larger number of rows of punctures (4-6), which is due to the punctures being more crowded, not only on the areola, but on the whole carapace.

The *earapace* is often provided with small and sharp *lateral spines*; they are sometimes obsolete, or replaced by tubercles, or even entirely absent.

Antennal seale generally slightly wider than in the typical form, and slightly longer.

Anteunal flagellum not differing greatly from that of the typical form, and quite variable in length. There are a few cases where it reaches to the end of the telson, and even slightly beyond, thus surpassing any case known in *C. bartoni*.

The first perciopods (Plate XL, Fig. 3), display remarkable and important differences from the typical form. The hand has nearly the same shape, but the fingers are less gaping, and meet all along their edges even in individuals of a considerable size (retention of juvenile character); it is only in very large specimens that they are distinctly gaping, but less so than in much smaller individuals of *C. bartoni*. The sculpture of the hand is much more strongly developed. The inner margin of the hand has a distinct and regular *double* row of tubercles. This double row is a very important character, and is noticeable in specimens from the size of about 30 mm. upward. In very young individuals it is obsolete, and becomes more and more distinct with advaneing age. Every specimen at hand, without exception, possesses this character, when the chelæ are normally developed; but it must be mentioned that in regenerated chelæ, which are always recognizable by their shape, this double row is sometimes indistinct or irregular. Further, there is a triangular depression both on the upper and lower side of the hand at the base of the

immovable finger. Both impressions are always present in large individuals; in younger ones they are indistinct, but are always marked by punctures, which are much crowded, and consequently by the denser hairs implanted in them. Traces of the impression on the upper surface are often seen in the typical form, but that of the lower surface is always absent, or marked only by a slight flattening of the surface. These two impressions give to the hand of this variety a very strongly marked marginal keel or ridge. The outer margin of the movable finger possesses a number of irregularly placed tubercles, indistinct, and restricted to the proximal part in young specimens, but very distinct, and occupying about two-thirds or three-fourths of the margin in old specimens. The longitudinal ribs of the upper surface of the fingers are always well developed, and there is hardly any tendency in older specimens for them to become obscure, chiefly in the case of the immovable finger, where this rib is always well marked on account of the strongly developed punctures of the depression accompanying it on the outside.

The armature of the *carpopodite* and the *meropodite* is almost identical with that of the typical form, but the carpopodite in old individuals is often provided with accessory low tubercles on the upper face. The spines of the meropodite are more distinct and more numerous; those on the distal upper margin (generally two of them) well developed, even in large individuals; those of the lower margin consisting of two to six in the outer row (two are rare, found only in young ones; in regenerated chelæ as many as eight); and seven to twelve in the inner row (as many as fourteen in regenerated chelæ).

All the other characters, including the *color* (see Plate B, Fig. 2), agree with the typical form. The color of the eggs (in the only specimen ever found with eggs, at Spartansburg) is prune-purple (VIII, 1), almost black.

There are in the collections of the Carnegie Museum one hundred and fortyseven specimens of this form, all of which are from Pennsylvania, with the exception of four, which are from Kentucky.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: Allegheny County, Chartiers Creek, Carnegie, (D. A. Atkinson coll.); Pine Creek, below Bakerstown Station, (D. A. Atkinson coll.); Squaw Run, near Aspinwall; Alleghany River, Sandy Creek; Alleghany River, Hulton; Little Bull Creek, Tarentum, (A. Koenig coll.); Puketta Creek, (A. Koenig coll.); McKeen County, Alleghany River, Larabee; Warren County, Crouse Run, Garland; Crawford County, Oil Creek and tributaries, Spartansburg; small tributary of Conneaut

Creek, Conneautville Station; *Erie County*, French Creek, Union City; Sixteen Mile Creek, Northeast, (Miss G. Kinzer coll.); Walnut Creek, Swanville; Elk Creek, Girard; Conneaut and Temple Creeks, Albion.

KENTUCKY : Small stream tributary to Rockcastle River, Livingston, Rockcastle County, (E. B. Williamson coll.).

PREVIOUS RECORDS.

Type locality : Humber River, Toronto, Ontario, Canada, (Girard).

CANADA: Don River, Toronto, Ontario, (Faxon); Weston, Ontario, (Faxon).

NEW YORK: Tributary of Racket River, near Tupper's Lake, St. Lawrence County, (Faxon); Canton, St. Lawrence County, (Faxon); Natural Bridge, Jefferson County, (Faxon); Fulton Lakes, Hamilton and Herkimer Counties, (Faxon); Petersboro, Madison County, (Faxon); Sodus, Wayne County, (Faxon); Genessee River, Rochester, Monroe County, (Hagen); Forestville, Chautauqua County, (Faxon).²⁰

PENNSYLVANIA : Squaw Run, near Aspinwall, Allegheny County, (Williamson); tributary of Alleghany River, Port Alleghany, McKean County, (Ortmann).

Оню: Big Jelloway Creek and tributaries, Knox County, (Osburn and Williamson); Oberlin, Lorain County, (Ortmann).

ILLINOIS: Decatur, Macon County, (Faxon).²¹

MARYLAND: Montgomery County, (Faxon).

VIRGINIA: Fredericksburg, Spottsylvania County, (Hagen); Wytheville, Wythe County, (Faxon).

New Localities :

PENNSYLVANIA: Waterford, Erie County, (Dep. Agriculture, Harrisburg).

MARYLAND: Deer Park, Garrett County, (P. R. Uhler coll., see below under C. diogenes. Footnote 27).²²

REMARKS :

In Pennsylvania this variety is well marked, and might safely be regarded as a species. Its chief characters are found in the shape of the rostrum and the sculpture of the hand. I never was in doubt as to this form, with the exception of young individuals (less than 30 mm. long), in which the hand does not show its characteristic features; but in such specimens the shape of the rostrum generally

²⁰ Hagen also gives: "Regis Lake, N. Y.", in the Adirondacks.

²¹ This locality should be confirmed, see Ortmann, 1905b, p. 135.

²² In Rough Run, West Winfield, Butler County, Pa., I found on June 20, 1904, several young specimens apparently belonging to this variety. I did not take them, expecting to get larger ones, in which hope I was disappointed. Thus this locality is somewhat doubtful.

gives a clue. This, however, is not the case in *very* young specimens, (less than 20 mm. long), and such I am unable to distinguish from the typical form.

The characters are slightly variable, as has been pointed out above, but this variety generally is very uniform in its characters in Pennsylvania. I have not found any variations worthy of special mention. With reference to the lateral spine of the carapace, there are specimens which show no trace of it, (young as well as old). In old specimens this spine is often tuberculiform, and in about half of the number at hand there is on each side a sharp, but always small lateral spine. In this respect there is no difference in the specimens of northwestern Pennsylvania from those found in Allegheny County.

It seems to me that the southern records for this variety (Maryland, Virginia, and also Kentucky)²³, do not refer to cxactly the same form which is found in the north (Canada, New York, northwestern Pennsylvania, northern Ohio). Hay (1899, p. 966), in the key to the species gives as one of the differential characters of *C. bartoni robustus*: "carapace cylindrical, sides nearly parallel as far forward as cervical groove, then curving abruptly to the base of rostrum," while, under *C. bartoni*, the carapace is described as " \ldots depressed, sides gently curving toward the front and rear." This cylindrical shape of the carapace is decidedly *not* present in our northern form; on the contrary, the depression of the carapace in our *robustus* is, if anything, more pronounced than in the typical *bartoni*; and our *robustus* agrees in this respect with Girard's type from Canada, preserved in the Academy of Natural Sciences, Philadelphia, and which has been examined by the writer.

On the other hand, our specimens from Kentucky seem to approach the form from Virginia and Maryland. The shape of the carapace is more cylindrical, as Hay describes it, G: H: B = 1:1.05 to 1.2:1.2 to 1.3. This shows that the width of the carapace at the branchial and hepatic regions is decidedly less, compared with the vertical diameter at the gastric region, than in the typical *bartoni*. There are other slight differences in the form from Kentucky: (1) the rostrum is not quite so narrow; (2) the lateral spine of the carapace is absent; (3) the punctures of the areola are not so crowded (about three rows), and are similar to those of *bartoni*; (4) the impressions of the hand are indistinct; (5) the double row of tubercles on the inner margin of the hand is different, the outer row being distinct, but the inner consisting of only a few more or less distinct irregular tubercles. All four specimens from Kentucky are comparatively small, (the largest is 54 mm. long), and thus the two last described characters may be due to age, although the specimens differ slightly

²³ Faxon, 1890; Hay, 1899; Williamson, 1905; Ortmann, 1905b.

from northern individuals of the same size. The other characters incline toward the typical *bartoni*, while the shape of the carapace varies to the other extreme.

A single male of the second form, about 60 mm. long, from Deer Park, Garrett County, Maryland, sent to me for examination by Dr. P. R. Uhler of Baltimore, was found under a lot of typical *C. bartoni*, (supposed to be *C. diogenes*). This male agrees fairly well with the specimens from Kentucky. The carapace is rather cylindrical; there are no lateral spines on the carapace; the punctures of the areola are like those of *C. bartoni*; the chelæ, which are unequal, and apparently both regenerated, have rather distinct impressions on the upper surface, but the inner margin has only one row of tubercles. The rostrum is of the *robustus*-type. Thus, of the characters of *robustus*, only the shape of rostrum and the impressions of the chelæ were present, all other characters being those of typical *bartoni*.

Specimens possessing a rather elongated rostrum, but with the other characters of typical *bartoni*, I have seen associated with individuals of the typical form taken at Gettysburg, Adams Co., Pa. (Dep. Agric., Harrisburg); but these I have recorded with typical *C. bartoni*. (See above, p. 385.)

It is very desirable that the southern form in Maryland, Virginia, Kentucky, and adjacent localities, should be investigated more closely. The records at hand, and the few, immature specimens the writer has seen, do not permit a final conclusion as to whether we have to deal in the south with a form differing from that in the north, or not. The same reason forbids us to restore our *C. robustus* to the rank of a species, which I surely would have done if the Pennsylvanian material alone were to be considered.

In Pennsylvania C. bartoni robustus is not always associated with C. bartoni. I found it thus in every case in Allegheny County, in Crawford County, and in Warren County. In McKean County I found it associated with C. obscurus in the Alleghany River at Larabee, but the typical C. bartoni was not there, although occurring not far away in small streams and springs. In Erie County C. bartoni was found only twice, in Elk Creek and Walnut Creek, associated with C. bartoni robustus, but then only a single individual of the former was found in each case. At Albion and Union City C. bartoni robustus alone was present, and I am sure of it, since I hunted for C. bartoni, but without success. The rich material from Northeast (forty-four specimens are now in the Museum, but many more were originally in the lot) did not contain a single C. bartoni. Thus it is beyond doubt that C. bartoni robustus is not infrequently found without the typical form, and chiefly so in the most northern and western sections of the state.

5. CAMBARUS (BARTONIUS) CAROLINUS Erichson.

(Plate A, Fig. 4; Plate XXXIX, Fig. 3a and 3b, and 9; Plate XL, Fig. 4).

Astacus (Cambarus) carolinus Erichson, 1846, p. 96.

Cambarus dubius Faxon, 1884b, p. 114; Faxon, 1885a, p. 70, Pl. 4, f. 3, Pl. 8, f. 7; Underwood, 1886, p. 368; Faxon, 1890, p. 624; Hay, 1899, p. 959, 965.

Cambarus carolinus Hay, 1902b, p. 38; Ortmann, 1905a, p. 393.

Cambarns (Bartonius) carolinus Ortmann, 1905b, p 120, 135.

Body robust, smooth, except for short hairs, chiefly on the chelæ in freshly moulted individuals.

Carapace subovate, not depressed, but rather compressed in comparison with the species described above. G: H: B = 1:1.07 to 1.1:1.1, that is to say, the vertical diameter and the transverse diameters of the hepatic and branchial regions are practically the same, the two transverse diameters being only slightly greater than the vertical. The greatest width of the branchial regions is well forward, immediately behind the cervical groove.

Cervical groove deep, not interrupted on the sides.

Areola distinctly longer than half of the anterior section of the carapace (a: p = 1: 1.65 to 1.74), very narrow (w: l = 1: 10 to 15), with only one, or rarely two, very irregular rows of punctures, which occasionally are almost entirely lacking.

Rostrum (Pl. XXXIX, Fig. 3a and 3b) slightly curved downward toward the tip, broad and short, never reaching beyond the distal end of the second joint of the peduncle of the antennula, but generally only to the middle of it, being sometimes even shorter than that. Upper surface slightly concave, with elevated margins. Margins straight, sub-parallel, or slightly converging toward the tip, suddenly contracted into a broad, short, triangular acumen. Basal angles of acumen rather sharp, but without any trace of marginal spines. These angles are emphasized by the sudden disappearance of the slight swelling of the lateral margins, which are not at all swollen on the acumen. Acumen pointed, but point short. Postorbital ridges short, almost parallel, ending bluntly anteriorly.

Surface of carapace punctate, granulated only on the hepatic region, and sometimes with a few indistinct granules immediately behind the cervical groove on the branchial region. No lateral spine. External orbital angle rarely or not at all marked, generally formed by a rounded or slightly angular, insignificant projection, but never with a spine. Branchiostegal spine formed by a small, often indistinct, tubercle.

Abdomen always distinctly shorter than the carapace, narrower than the latter in the male, almost as wide as the carapace in the female. Anterior section of telson

on the posterior lateral corners with one or two spines. Posterior section semi-elliptical, distinctly wider than long, about as long as the anterior section.

Epistoma with posterior part comparatively long, hardly one and one-half times as broad as long; transverse groove indistinct and close to posterior margin; anterior median depression also indistinct, and thus the posterior part of the epistoma appears rather flat and smooth. Anterior section constricted at base, semi-circular or semi-elliptical or subquadrate, rarely with a median anterior point, often more or less truncate anteriorly, or even slightly emarginate. Transverse diameter never greater than longitudinal, as great as the latter or shorter.

Antennula with a small tubercle on the lower margin of the basal joint. Antennal peduncle without distinct spines or tubercles on the two proximal, joints.

Antennal scale short and small, slightly longer than the rostrum, and not reaching beyond the distal end of the fourth joint of the antennal peduncle. Spine of outer margin strong. Laminar part only slightly wider than the spine.

Flagellum short, not reaching beyond the third abdominal segment in the male, and not beyond the second segment in the female, but often hardly longer than the carapace.

First perceiopods (Pl. XL, Fig. 4) short, not very robust, not undergoing much change with age, and not differing much according to sex. Hand ovate, broad and depressed. Surface punctate. Inner margin of palm convex, with a single row of distinct tubercles, larger proximally; occasionally there is a second, incomplete row inside of and parallel to this. Outer margin smooth and rounded proximally for a short distance, but soon becoming angular and forming a distinct ridge along the edge in the region of the base of the immovable finger. This ridge has a regular row of deep punctures, giving the distinct appearance of serrations along the outer margin of the hand. Fingers as long as, or slightly longer than the palm, slightly gaping at the base in both young and old individuals, straight. Outer margin of movable finger with punctures, but very rarely with tubercles. Cutting edges with a few irregular tubercles in the proximal half. Upper surface of each finger with a low rib, bordered by rows of punctures.

Carpopolite slightly longer than wide, about as long as the palm, with a deep longitudinal sulcus above. There is always a strong, more or less pointed, spine on the inner margin, directed obliquely forward, and a strong, often spiniform, conical tubercle in the middle of the anterior margin of the under side, (rarely obsolete). The tubercle at the lower articulation with the hand is low and indistinct. Rarely there are accessory tubercles, which, however, are never spiniform. The most frequent are a proximal tubercle on the inner margin, and one between the two larger spines first mentioned, and another just behind the base of the large spine of the inner margin.

Meropodite smooth, with 1-3 indistinct tubercles near the distal end of the upper margin, often entirely obsolete. Lower side with two rows of spiniform tubercles. The outer row consists of 2-6 (if only 2, they are followed by a few undulations produced by punctures); the inner consists of 6-11 tubercles. Outer articular tubercle with carpopodite without spine. All spines of the first pereiopods are indistinct in very young specimens.

Ischiopodite of third pereiopod hooked in the male. Hook of the male of the first form strong, subconical.

Coxopodite of fourth pereiopod in the male with a prominent, blunt, and slightly compressed subconical tubercle.

First pleopods of the male (Plate XXXIX, Fig. 9) similar to those of *C. bartoni*. Annulus ventralis of the female likewise of the type of *C. bartoni*, but less transverse, and the posterior margin more swollen and elevated, while the anterior is hardly elevated at all, but depressed.

Size. — The largest male of the first form at hand is from Dunbar, Fayette County, and measures 67 mm. in length. The largest female is from Ohiopyle, Fayette County, and measures 80 mm. in length.

Color (Plate A, Fig. 4). — Whole body rather uniformly orange-chrome (Ridgway, 1886, VII, 13) to chinese-orange (VII, 15), very brilliant in fresh shells, shading to orange-rufous (VII, 12) and cream-color (VI, 20) on the sides. Color most intense on anterior part of carapace and on the claws. Abdomen orange-chrome, shading to salmon-color (VII, 17) or ferrugineous (IV, 10), or ochraceous-buff (V, 13). Chelæ varying from orange-chrome to saturn-red (VII, 16). Legs chinese-orange to salmon-color and ferrugineous. Often a brown or blackish coat of mud covers a great part of the body, obscuring the colors. The color of young specimens is semitransparent, with more or less red prevailing, but the rostrum and chelæ are always distinctly red. Color of eggs salmon (VII, 17) to salmon-buff (IV, 19).

There are one hundred and thirty-eight specimens in the Carnegie Museum; ninety-three from Pennsylvania, thirty-six from West Virginia, and nine from Maryland.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: Westmoreland County, Jones Mills; Fayette County, Dunbar; Indian Creek; Rainier Park, Ohiopyle; Somerset County, Windber; Listie; Rockwood; Myersdale.

MARYLAND: Garrett County, Selbysport.

WEST VIRGINIA: Preston County, Reedsville; Tucker County, Parsons; Mineral County, Schell.

PREVIOUS RECORDS.

Type locality : Greenville, Greenville County, S. C., (Erichson and Faxon, 1885*a*, pp. 9, 56).

TENNESSEE : Cumberland Gap, Claiborne County, (Faxon).

VIRGINIA: Pennington Gap, Lee County, (Faxon).

WEST VIRGINIA: Southwestern West Virginia, (Hay); Terra Alta (Cranberry Summit), Preston County, (Faxon).

INDIAN TERRITORY : Cherokee Nation, (Faxon).²⁴

New Locality:²⁵ Blowing Rock, Watauga County, North Carolina, (J. P. Moore coll., Acad. Nat. Sci. Philadelphia).²⁶

REMARKS:

This species, the Red Crawfish of the mountain regions, occupies, next to *C. propinquus*, the smallest area in this state. Its morphological characters are very uniform, not only in this state, but also in the neighboring parts of West Virginia and Maryland. The chief variations, as already mentioned in the description, are found in the armature of the chelipeds, but they keep within comparatively narrow limits. The rostrum, which is quite variable in *C. bartoni*, is here very constant, only the degree of convergence of the lateral margins and the length of the acumen varying to a certain extent, (See Pl. XXXIX, fig. 3*a* and 3*b*.) Of course, we must disregard monstrosities, under which head I place two cases, (from Dunbar and Parsons), where the rostrum has almost no acumen at all, being rounded off apically.

The armature of the meropodite and carpopodite varies as described above; the carpopodite in particular showing a various number of tubercles, though they never become spiniform as in *C. monongalensis*. The lower outer margin of the meropodite has always more than one spine, when spines at all are visible, which is generally not the case in very young individuals.

²⁶ These specimens (collected June, 1893, and, according to Professor Moore's recollection, dug out of holes) agree in all essential points with our material, only the rostrum is narrower.

²⁴ This locality needs confirmation, see Ortmann, 1905b, p. 135.

²⁵ This species is abundant in certain parts of Somerset and Fayette Counties, Pa., and well known to the natives-I have seen chimneys in abundance at Confluence, Somerset County, which undoubtedly belong to this species, but was not able to secure specimens, my time being limited. I have seen a specimen at Flanigan, 4 miles north of Somerfield, Fayette Co., and one from Humbertston, Fayette Co. (O. T. Cruikshank coll.). Reports received from farmers, always emphasizing the red color and burrowing habits of the crawfish in question, are the following : Great Meadow Run, west of Ohiopyle, Fayette County ; Millrun, Fayette County ; Ursina, Somerset County ; Salisbury, Somerset County.

I think I have observed that in specimens from the south (Maryland and West Virginia) there is a more pronounced tendency to develop a second row of tubercles at the inner margin of the hand. Such specimens, with a few additional tubercles, occur also in Pennsylvania, but in West Virginia they are more frequent, and the additional row becomes more distinct and more regular. There is moreover a specimen from Parsons, W. Va., in which traces of a third distal row are visible. On the other hand specimens with one row only are also found in West Virginia.

No interesting freaks or monstrosities have been observed.

6. CAMBARUS (BARTONIUS) MONONGALENSIS Ortmann.

(Plate B, Fig. 4. Plate XXXIX, Fig 4a, 4b and 10. Plate XL, Fig. 5.)

Cambarus dubius Williamson, 1901, p. 11, (non dubius Faxon). Cambarus monongalensis Ortmann, 1905a, p. 395. Cambarus (Bartonius) monongalensis Ortmann, 1905b, p. 120.

This species being closely allied to *C. carolinus*, the description will be given in terms of comparison with the latter.

General shape of body, carapace, cervical groove, and areola identical with that in C. carolinus. G: H: B = 1:0.9 to 1.1:1.1 to 1.3.

Rostrum (Pl. XXXIX, Figs. 4a and 4b) markedly different from that of C. carolinus. It is as long as that of the latter species, or slightly shorter in the average, never reaching beyond the middle of the second joint of the antennula, and is uniformly narrower. The upper surface is concave. The margins are less sharply elevated, the elevation decreasing gradually to the apex. Margins distinctly converging, and contracted to form the short, triangular acumen, but the contraction is not so sudden as in C. carolinus, so that the angles at the base of the acumen are not so sharp, but rounded. Acumen with short point. Postorbital ridges short and rather indistinct, distinctly divergent posteriorly.

Sculpture of carapace and other details as in *C. carolinus*. The *abdomen* and *telson* are also identical, but the lateral corners of the anterior section of the telson have only one spine.

Epistoma similar to that of *C. carolinus*, but the truncated (subquadrate) shape prevails in the anterior section, which has often a small median anterior point.

Antenna and antennula similar to those of *C. carolinus*, but antennal scale shorter, not much longer than the rostrum, and reaching only to the middle of the fourth joint of the antennal peduncle.

First pereiopods (Pl. XL, Fig. 5) in general shape similar to those of *C. carolinus*, but hand not quite so broad, and there are important differences in the armature. The inner margin of the hand invariably has only one, but a distinct, row of tuber-

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cles. The outer margin is rounded, with no indication of angulation, and entirely lacks the servations of *C. carolinus*, the punctures producing the latter forming in this species no regular row.

The *earpopolite* is much more spinous. The large spine of the inner margin is well developed. The spine in the middle of the anterior margin of the under side is tuberculiform, and the tubercle at the lower articulation with the hand is insignificant. But there always are additional distinct spines, which are well developed, although smaller than the large spine of the inner margin. A spine on the proximal end of the inner margin is always present, and also a spine between the large spine of the inner margin and the anterior tubercle of the lower side. (If the latter spine is missing, the claw has been regenerated.) Often there are other spines. The proximal spine of the inner margin may be double, and there may be one or several spines or tubercles near the base of the large spine of the inner margin, anterior or posterior to it.

Meropodite with the distal tubercles of the upper margin very indistinct, generally missing. The outer lower margin is formed by a smooth keel, which has in most cases only one small tubercle near the distal end, which may be obsolete. In rare instances there are two tubercles. If there are more, the claw has been regenerated. The inner lower margin has a row of 6–12 spiniform tubercles; if less, the claw has been regenerated.

All the other organs are similar to those of *C. earolinus*, more particularly the first pleopods of the male (Pl. XXXIX, fig. 10) and the annulus of the female.

Size. — The largest male of the first form, from Edgewood Park, Allegheny County, is 68 mm. long; the largest females (same locality and Monaca, Beaver County), are 76 mm. long.

Color (Pl. B, Fig. 4). — In specimens with fresh shells the middle of the carapace and abdomen is of a beautiful marine-blue (Ridgway, 1886, IX, 2); the hepatic and branchial regions are cyanine-blue (IX, 3) and ehina-blue (IX, 13), shading toward the lower margin to pale-blue (IX, 16). The marine-blue of the abdomen is restricted to the anterior parts of the segments; the posterior parts and the epimera are china-blue shading to pale-blue. Margins of rostrum maroon-purple (VIII, 9). The hand is cyanine-blue above, shading toward the lower side to eobalt-blue (IX, 12), azure-blue (IX, 15) and pale-blue. At the base of the dactylopodite there is a good deal of royal-purple (VIII, 7). The dactylopodite is cyanine-blue, the outer margin violet (VIII, 10). The finger-tips are orange-vermilion (VII, 12), shading proximally to salmon-color (VII, 17) and whitish. The carpododite of the chelipeds is marineblue, shading to cyanine-blue and French-blue (IX, 6). Tubercles and spines of

hand and carpopodite pale vinaceous-pink (lighter than IV, 21). Basal joints of antennæ cyanine-blue; flagellum annulated dahlia-purple (VIII, 2) and very pale lilac (lighter than VIII, 19). Pereiopods pale-blue, upper edges shading to china-blue, near the bases white. Lower side of body whitish, on the abdomen suffused with china-blue and pale-blue.

These brilliant colors fade more or less in old specimens, but the *marine-blue* always remains the ground-color. A brownish or blackish deposit of mud often obscures the colors, and such specimens often appear *blackish-blue* all over.

Young individuals are semitransparent, with a distinct *pale-blue* hue on the abdomen and chelæ, and *heliotrope-purple* (VIII, 18) on the carapace.

Distinct color varieties are rare, and the few observed will be mentioned below. The color of the newly laid eggs is *hazel* (IV, 12) or *ochraceous* (V, 7); later on they are *vinaceous-buff* (V, 15) on one side, *pinkish-white* on the other.

The Carnegie Museum possesses two hundred and seventy-nine specimens of this species, two hundred and thirty-six of which are from Pennsylvania, and forty-three from West Virginia.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: Westmoreland County, Hill, (opposite Leechburg); Braeburn; Dundale; Jeanette; Allegheny County, south of Logan's Ferry, (C. V. Hartman coll.); Hulton, (R. Dornberger coll.); Wilkinsburg, (D. A. Atkinson coll.); Edgewood Park, (type locality); Nine-Mile Run, Pittsburgh; Fern-Hollow, Pittsburgh; Schenley Park, Pittsburgh; Squaw-Run, near Aspinwall, (D. A. Atkinson); North Versailles Township, (opposite Stewart); Jack's Run and Long Run, South Versailles Township; Boston, (D. A. Atkinson); Thompson's Run, Kennywood, (F. E. Kelley coll.); Carnegie, (D. A. Atkinson); Moon Township, (A. T. Shafer coll.); Lashell's Hollow, Moon Township: Beaver County, Doctor Heights, Monaca; Washington County, Francis Mine near Burgettstown; Taylorstown; Monongahela City; West Brownsville; Fayette County, Smithfield; Cheat Haven; Greene County, Deer Lick.

WEST VIRGINIA: Hancock County, Congo; Hollidays Cove; Brooke County, Colliers; Ohio County, Elm Grove; Marshall County, Cameron; Nuss; Monongalia County, Morgantown.

PREVIOUS RECORDS.

The only previous records are those given by Williamson (as *C. dubius*), Schenley Park and Fern Hollow, Pittsburgh, and Moon Township, Allegheny County.

ADDITIONAL LOCALITY.

The writer has seen this species at Sandy Creek, Allegheny County, Pa.

REMARKS.

The Blue Crawfish is rather abundant in the region indicated by the above localities, and apparently represents a geographical differentiation of *C. carolinus*, the Red Crawfish. The points in which it differs from the latter species, aside from color, are slight, but are constant according to my observations.

The rostrum is markedly different from that of *C. carolinus*, although slightly variable. It always is smaller than that of the latter species and narrower, with less distinctly marked lateral angles. The lateral margins are swollen, but the swelling is less marked, and docs not suddenly decrease at the lateral angles. The degree of convergence of the margins is variable, but generally much more pronounced than in the Red Crawfish; cases like that figured in Plate XXXIX, Fig. 4b, are rather rare, in fact, this case forms the extreme in this direction.

In the shape of the hand, the rounded outer margin and the absence of serrations on it are other striking characters of this species; and the carpopolite is distinguished by the larger number of spiniform tubercles, as described above. The outer lower margin of the meropodite generally has a blunt and smooth keel, with only one small tubercle near the distal end (which may be absent). Among my material I had only ten specimens which revealed an exception, where two such tubercles were present, and in only two of them were these tubercles present on both chelipeds. In the others they occurred only on one side. There are instances in which a large number are found, but always in claws which have been regenerated.

Aside from the slight variations indicated above only a few exceptional cases have been encountered in which marked deviation from the above description of the prevalent colors occurs. The blue ground-color is always present on the anterior part of the carapace and the chelæ. In a rare variation, which has been observed about half a dozen times, the ground-color of the posterior part of the carapace and parts of the abdomen are more or less purplish (*auricula-purple*, VIII, 3). Furthermore a single adult female was found at Monaca in which all red tints were absent; the blue of the body was very clear, the margins of the rostrum were blue like the carapace, the finger tips were whitish, all spines and tubercles were pure white, and the antennal flagellum was a pure blue. Specimens in which the margins of the rostrum have the same shade of blue as the carapace are not infrequent.

Other freaks are occasionally found, as for instance a specimen without an acumen on the rostrum, the latter being evenly rounded off; a specimen with the immovable finger of the left hand with a double tip, the outer one the larger, and a specimen with the movable fingers of both hands only half as long as usual, thick, short, and conical. Such cases apparently are due to some previous injury, and suggest nothing of special interest.

All the variations mentioned above are rare and are not restricted to certain parts of the range of the species, so that we do not distinguish any regional varieties.

7. CAMBARUS (BARTONIUS) DIOGENES Girard.

(Plate A, Fig. 3; Plate XXXIX, Fig. 11; Plate XL, Figs. 6 and 7.)

Cambarus diegenes Girard, 1852, p. 88; Faxon, 1884b, p. 144; Abbott, 1884, p. 1157; Faxon, 1885a, p. 71; Faxon, 1885b, p. 359; Faxon, 1885c, p. 140; Underwood, 1886, p. 368; Faxon, 1890, p. 624; Ortmann, 1891, p. 12; Hay, 1896, p. 489, Fig. 7; Faxon, 1898, p. 650; Osburn & Williamson, 1898, p. 21; Williamson, 1899, p. 20, 48; Hay, 1899, p. 959, 961; Harris, 1900, p. 267; Williamson, 1901, p. 11; Hay, 1902a, p. 235; Ortmann, 1905a, p. 398.
Cambarus obesus Hagen, 1870, p. 81, pl. 1, f. 39–42, pl. 3, f. 163, pl. 9; Smith, 1874, p. 639; Forbes, 1876, p. 5, 19; Bundy, 1877, p. 171; Bundy, 1882, p. 183; Bundy, 1883, p. 403.

Cambarus diogenes ludoricianus Faxon, 1884b, p. 144 ; Hay, 1899, p. 959, 962. Cambarus dubius Osburn and Williamson, 1898, p. 21, (non dubius Faxon).

Cambarus (Bartonius) diogenes Ortmann, 1905b, p. 120, 135.

Body robust, smooth, except for short hairs, chiefly on the chelæ in fresh shells; the hairs also to a certain degree persist upon the hand and fingers in older individuals.

Carapace subovate, not depressed, but rather compressed. G: H: B = 1:0.88 to 1.0:1.06 to 1.2; that is to say, the transverse diameter of the carapace is very slightly greater than the vertical, at the hepatic region sometimes even less. Greatest width of branchial regions well forward, not far from the cervical groove.

Cervical groove deep, not interrupted on the sides.

Areola distinctly longer than half of the anterior section of the carapace (a:p = 1:0.61 to 0.75), very narrow, and generally obliterated in the middle; that is to say, the two lines bordering the branchial regions are in contact in the middle of the carapace. In rare instances a small space is left between them, upon which there is no room for punctures.

Rostrum more or less lanceolate, rather narrow, but not very long, reaching hardly beyond the distal end of the second joint of the peduncle of the antennula, being often shorter. Upper surface slightly concave, with elevated margins. Margins not much swollen, the swelling gradually disappearing toward the tip, converging, straight, or slightly convex, contracted to form a short triangular acumen. Basal angles of acumen indistinct, rounded, without any trace of marginal spines.

Point of acumen short. Postorbital ridges short, terminated bluntly in front, slightly divergent posteriorly, ending in a low, indistinct swelling.

Surface of carapace punctate, slightly granulate on the hepatic region, and with a few granules on the branchial region, immediately behind the cervical groove. No lateral spine. External orbital angle present, distinct, angular or rounded, but without tubercle or spine. Branchiostegal spine formed by a small, often indistinct, tubercle.

Abdomen about as long as the carapace, or very slightly shorter or longer, narrower than the carapace in the male, markedly wider and about as wide as the carapace in the female. Anterior section of *telson* with 1-3 (generally 2) spines on the posterior lateral corners. Posterior section semi-elliptical, slightly wider than long, and about as long as the anterior section.

Epistoma similar to that of *C. carolinus* and *monongalensis*, comparatively long and narrow, rather flat, and with the anterior section semi-circular, semi-elliptical, or truncate and subquadrate, with or without median point, and about as long as wide.

Antennula with a small tubercle on the lower margin of the basal joint.

Antennal peduncle without spines or tubercles on the proximal joints.

Antennal scale small and short, slightly longer than the rostrum, and reaching to the base of the fifth joint of the peduncle of the antenna. Spine of outer margin strong; laminar portion not much wider than the spine, its inner margin parallel to the outer margin of the spine for a considerable distance.

Flagellum short, often only as long as the carapace or even shorter, never reaching beyond the second abdominal segment.

First pereiopods (Pl. XL, Fig. 6) stout and very robust in old individuals; not much different in the male and female, except for their very large size in old males. Hand ovate, broad, depressed. Surface punctate. Inner margin of palm convex, with two irregular rows of tubercles, and a few scattered tubercles on the upper surface near the marginal rows. Outer margin smooth, rounded proximally, slightly angular distally. Fingers at least one and one-half times as long as palm (the latter measured from articular tubercle with carpopodite to articular tubercle with dactylopodite), gaping at the base, straight both in young and old specimens. Cutting edges with a number of strong but irregular tubercles; one tubercle at about the middle of the edge of each finger is generally the largest. Outer margin of movable finger with more or less distinct tubercles at the proximal end. Upper surface of each finger with a low longitudinal rib, bordered by rows of punctures.

Carpopodite about as long as wide, shorter than palm, with a deep longitudinal

sulcus above, and a few more or less distinct tubercles between sulcus and inner margin. A strong pointed spine in the middle of the inner margin, straight, and directed obliquely forward. A tubercle or spine on anterior margin of lower side, and a low tubercle at articulation with hand. A few additional tubercles may be present on the inner margin and the lower side, but they are very rarely spiniform.

Meropodite smooth, with 1–3 indistinct tubercles near the distal end of the upper margin. Lower side with an outer row of 1–4, and an inner row of 7–11 spiniform tubercles.

Ischiopodite of third pereiopods hooked in the male; hooks in the male of the first form strong, subconical.

Coxopodite of fourth pereiopods with a strong, slightly compressed tubercle.

First pleopods of male (Pl. XXXIX, Fig. 11) similar to those of *C. bartoni*, the tip of the inner part, however, tapering gradually to the point.

Annulus ventralis of female similar to that of C. carolinus.

Size. — The largest specimens at hand from the eastern part of the state are a male (first form) and a female from Ridley Park, both 83 mm. long. From the western part of the state I have a male of the first form from Nine-Mile Run, Pittsburgh, which measures 92 mm. in length, and a male of the second form from Mill-vale, Allegheny County, which is 93 mm. long. The largest female is from Nine-Mile Run, and measures 97 mm. in length.

In the west this species attains a much larger size. The maximum length has been recorded by Hagen, 4.5 in. = 115 mm. However, the Carnegie Museum possesses a male of the first form from Bluffton, Wells County, Indiana (collected by E. B. Williamson), which is now (in alcohol) 122 mm. long, but measured 124 mm. when alive.

Color (Pl. A, Fig. 3). — The color is rather variable within certain limits, but the ground-color is similar to that normally seen in crawfishes, brownish or greenish.

Ground-color on carapace and abdomen from *olive-green* (Ridgway, 1886, X, 18) to raw-umber (III, 14), mummy-brown (III, 10) and ferrugineous (IV, 10), shading on the sides through drab (III, 18) or russet (III, 16) to fawn-color (III, 22) and whitish. Margins of rostrum rufous (IV, 7) or ferrugineous (IV, 10). The hand is tawny-olive (III, 17) to burnt sienna (IV, 6) and rufous, shading to olive-yellow (VI, 16) toward the outside. At the bases of the fingers there is often a distinct shade of olive-green (X, 21). The finger tips are rufous, the tubercles of the hand cream-buff (V, 11) or whitish. The legs are ochraceous-buff (V, 10) with olive-buff (V, 11), or russet (III, 16) with olive-green (X, 18) at the joints. Lower side of body pale rufous or pale orange-buff (VI, 22), or whitish. The antennal flagellum is annulated dark olive-

green and whitish. The relative amount of green and brown changes very considerably with different specimens, but in general we may say that green prevails in the young, and brown in older specimens.

Color of newly laid eggs buff (V, 13); when more advanced prune-purple (VIII, 1), or indian-purple (VIII, 6) on one side, cream-color (V. 20), or dirty-white on the other.

In the Carnegie Museum there are altogether three hundred and twenty-three specimens of this species, of which twenty are from eastern and two hundred and sixty-six from western Pennsylvania. Two specimens are from Maryland, five from West Virginia, twenty-four from Indiana and three from Iowa; while one specimen is from each of the states of Delaware, Ohio, and Kansas.

DISTRIBUTION.

LOCALITIES REPRESENTED IN THE CARNEGIE MUSEUM.

PENNSYLVANIA: Bucks County, Penns Manor; Philadelphia County, Essington; Delaware County, Ridley Park; Marcus Hook; Greene County, Waynesburg; Rice's Landing; Fayette County, Smithfield; Dunbar; Pennsville; Washington County, Francis Mine near Burgettstown; Beaver County, Baden; Racoon Township; Allegheny County, Troup's Retreat, Moon Township, (E. B. Williamson coll.); Stowe and Neville Townships, (Atkinson, Graf, and Williamson coll.); Edgeworth, (Mrs. E. Courtney coll.); Westview, (D. A. Atkinson coll.); Millvale; Fern Hollow and Nine-Mile Run, Pittsburgh; Schenley Farm, Pittsburgh, (F. E. Kelly coll.); Silver Lake, Pittsburgh, (E. B. Williamson coll.); Bruce's Ice Pond, Pittsburgh, (Atkinson and Williamson coll.); Carnegie, (D. A. Atkinson coll.); Jack's Run, North Versailles Township; Rankin, (O. T. Cruikshank coll.); Squaw Run, near Aspinwall; Montrose; Harmarville; Russelton; between Gibsonia and Bakerstown Station; Thornhill; Westmoreland County, Donohoe; New Alexandria; Dundale; Reservoir of McGee Run, Derry; Blairsville Intersection; Livermore; Kiskiminetas Junction; Indiana County, Homer; Creekside; Jefferson County, Punxsutawney; Armstrong County, Long Run, Avonmore Station; Kittanning; Butler County, Renfrew; Branchton; Lawrence County, Wampum; Mercer County, Mercer.

DELAWARE: Sussex County, Seaford, (S. N. Rhoads coll., exch. Ac. Nat. Sci., Philadelphia).

MARYLAND: Kent County, Chestertown, (E. G. Vanatta coll., exch. Ac. Nat. Sci., Philadelphia).

WEST VIRGINIA: Hancock County, Congo; Brooke County, Colliers; Wetzel County, New Martinsville.

OHIO: Franklin County, Columbus, (E. B. Williamson coll.).

INDIANA: Wells County, Bluffton; Twin Lakes; Craigville; Liberty Center; Uniondale; Blackford County, Hartford City; De Kalb County, Newville (all coll. by E. B. Williamson).

Iowa: Greene County, Cooper, (J. B. Hatcher coll.); Lee County, Denmark (R. L. Baird coll.).

KANSAS: Douglas County, Lawrence, (S. Prentice coll.).

PREVIOUS RECORDS.

Type Locality: Washington, D. C., (Girard).

NEW JERSEY: Trenton, Mercer County, (Abbott).

MARYLAND: Worcester County, (Faxon); Dorchester County, (Faxon); Caroline County, (Faxon); Baltimore County, (Faxon); St. Mary County, (Faxon).²⁷

VIRGINIA: Accomac County, (Faxon); Northampton County, (Faxon); Alexandria County, (Faxon); Prince William County, (Faxon); Fredericksburg, Spottsylvania County, (Faxon); Petersburg, Dinwiddie County, (Hagen).

NORTH CAROLINA: Kingston, Lenoir County, (Faxon); Wilmington, New Hanover County, (Faxon).

PENNSYLVANIA: Derry, Westmoreland County, (Faxon); Pittsburg, Allegheny County, (Williamson).

OHIO: Oberlin, Lorain County, (Osburn and Williamson); Knox County, (Williamson); Columbus and Lockbourne, Franklin County, (Faxon); Montgomery County, (Williamson).

MICHIGAN: Detroit, Wayne County, (Faxon).

KENTUCKY: Louisville, Jefferson County, (Faxon); Bee Spring, Edmonson County, (Faxon); Mammoth Cave, Edmonson County, (Hay).²⁸

INDIANA: Kendallville, Noble County, (Bundy); Riverside, Laporte County, (Faxon); Kokomo, Howard County, (Faxon); Mechanicsburg, Henry County, (Bundy); Irvington, Marion County, (Hay); North Salem, Hendricks County, (Hay); Greencastle, Putnam County, (Hay); Bloomington, Monroe County, (Hay); Knox County, (Faxon).

²⁷ Faxon also gives Deer Park, Garrett County, (Coll. P. R. Uhler). I have doubted (1905b, p. 136) the correctness of this locality. In order to be sure I have asked Dr. P. R. Uhler of Baltimore to send to me the specimens upon which this record was founded, and Dr. Uhler very kindly complied with my request. There were two males of the second form and four females in the lot, all belonging to *C. bartoni*, and representing the typical form, with the exception of one male, which I have identified with the southern form of *C. bartoni robustus* (see above, pp. 391 and 393). Thus this record (Deer Park) for *C. diogenes* is to be dropped.

²⁸ The localities in Jefferson and Edmonson Counties are given by Faxon with a ?; but Hay's record of this species from Mammoth Cave tends to confirm their correctness.

ILLINOIS: Chicago, Cook County, (Hagen); Evanston, Cook County, (Hagen); Lawn Ridge, Marshall County, (Hagen); Abingdon, Knox County, (Faxon); Decatur, Maeon County, (Faxon); Belleville, St. Clair County, (Hagen).

WISCONSIN: "Abundant in Wiseonsin," (Bundy); Raeine, Raeine County, (Faxon); Green County, (Faxon); Appleton, Outagamie County, (Faxon).

MINNESOTA: Fort Snelling, Hennepin County, (Faxon).

Iowa: Davenport, Scott County, (Faxon); Delhi, Delaware County, (Faxon); Belmond, Wright County, (Faxon).

MISSOURI: St. Louis, St. Louis County, (Faxon); Carroll County, (Faxon).

KANSAS: Leavenworth, Leavenworth County, (Faxon); Lawrenee, Douglas County, (Harris).

ARKANSAS: Paragould, Greene County, (Faxon); Fayetteville, Washington County, (Faxon).

MISSISSIPPI: Montieello, Lawrenee County, (Hagen).

LOUISIANA: New Orleans, (Hagen).

WYOMING: Cheyenne, Laramie County, (Faxon).

COLORADO: Clear Lake, (Faxon)²⁹; Boulder, Boulder County, (Harris)³⁰.

REMARKS.

Cambarus diogenes occupies two areas, in the United States, which, according to our present knowledge, are separated from each other; a western and an eastern. Both areas enter Pennsylvania, the one extending over a large portion of the southwestern territory of this state, the other being much smaller and restricted to the southeastern extremity.

I have closely studied the material at hand, and have found eertain differences between eastern and western specimens, which however are very slight, and not always constant; yet a tendency to a morphological separation between the eastern and western forms seems to be indicated. Faxon (1885a, p. 72) has already called attention to some of these differences.

The description given above refers chiefly to the *eastern* form of this species. Specimens from western Pennsylvania show the following differences :

1. Areola in most cases not entirely obliterated. There are, indeed, cases in the eastern form where the two lines bordering the branchial regions are not in contact, but they are rare. In western Pennsylvania the latter condition is rather the rule, although specimens in which both lines unite, forming in the middle only one line,

²⁹ Location unknown to the writer.

³⁰ Professor T. D. A. Cockerell has sent to me for examination a young male collected October 7, 1905, in a small stream near Boulder. Although very small it clearly belongs to this species.

are by no means absent. There is some variability in this character. Generally a very narrow space is left between the two lines, which does not leave room for any punctures. But it is a curious fact that the pareola is widest in specimens from Fayette and eastern Greene Counties. In these localitics specimens with an entirely obliterated areola are exceedingly rare, and specimens with the areola so wide that there is room for one irregular row of punctures are rather frequent, (Pennsville, Dunbar, Smithfield, Fayette County; Rice's Landing, Greene County). Such specimens with punctures on the areola, which is accordingly wide, are scarcely found anywhere else. I possess only one from Pittsburgh.

2. Rostrum, in all eastern specimens at hand, with a more or less distinct acumen. In the western form there is a distinct tendency to render the acumen obscure. Indeed there are many specimens which have the acumen exactly as in the eastern form, but there are as many where it is not marked, the margins converging evenly to the tip. In such specimens the rostrum assumes a rather regular lanceolate shape, and appears somewhat more elongate and narrow. However, it is actually not longer than in the eastern form.

3. The swelling at the posterior ends of the *postorbital ridges* is sometimes more distinct in western specimens.

4. In our western form the *external orbital angle* is rarely angular, but generally blunt or rounded. In some cases it is very slightly developed.

5. There are specimens in western Pennsylvania where the posterior section of the telson is longer and more tapering. In extreme cases this is rather striking, the posterior section being distinctly longer than the anterior, and longer than wide. This latter condition is never found in eastern specimens. On the other hand there are many western specimens which do not differ in this respect from the eastern, and many transitional conditions have been observed.

6. Antennal scale in the western form often slightly wider than in the eastern, and with a stronger spine. This difference, however, is very slight.

7. Chelæ in the western form (Pl. XL, Fig. 7) of slightly different shape, but this difference always holds good, provided the chela has not been regenerated, and is otherwise normally developed. The inner margin of the palm in the eastern form has always two rows of tubercles, while on the upper surface there are at the best only a few minute, scattered tubercles, chiefly near the base of the dactylopodite. In the western form the two rows of tubercles are also generally distinguishable, but often the inner row is irregular, and merges into the scattered tubercles present upon the inner half of the upper surface. These latter tubercles are invariably present, and are much more numerous than in the castern form. The dactylopodite

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of the western form is generally shorter. While in the eastern form it is at least one and one-half times as long as the palm, in the western form this relation is the maximum, and is due to a proportionally heavier and stronger development of the palm as compared with the fingers. (This does not hold good for regenerated chelæ, in which the dactylopodite always is considerably longer in proportion to the palm.)

The tubercles of the cutting edge of the dactylopodite are slightly different in both forms. In the eastern the third or fourth is generally much larger, and, just before it, there is a gap, as if one tubercle were suppressed. This produces a distinct excision at the base of the finger, which is always more or less marked, even in rather young individuals, so that the fingers always appear gaping at the base (Pl. XL, Fig. 6). In the western form the fourth or fifth tubercle is larger than the rest, but there is no distinct gap anterior to it, the three or four proximal tubercles being rather equidistant. They decrease slightly in size from the first to the fourth, so that a slight emargination is indicated. But this emargination and the large tubercle following it are well distinguishable only in larger individuals; in younger specimens they are rather indistinct, or entirely wanting, so that the basal gap is absent, and the fingers are in contact all along their edges.

The differences in the relation of dactylopodite to palm, and in the tubercles of the dactylopodite, give to the whole chela of the western form a different aspect, the hand appearing rather more massive with shorter fingers. (See Pl. XL, Figs. 6 and 7.)

8. The colors in western specimens are more vivid, and with more contrast. Eastern specimens are more uniformly russet or olive-green, with no oil-green at the base of the fingers, while the latter tint is very characteristic of the western form, at least in specimens of a certain size. Old western specimens, when fresh, are rather brilliantly colored.

I think I am able to recognize and to distinguish eastern and western specimens, chiefly by the help of the characters of the chelæ, if the latter are normally developed; but I do not know whether it would be advisable to distinguish both forms by varietal names. The latter may be necessary in future, when the forms of *C. diogenes* from the regions west of Pennsylvania have been more closely studied. I think I am able to see certain differences in the western specimens in our collections, but the material is too poor to be sure of it.

No remarkable freaks or malformations have been observed in this species, with the exception of a few color variations. They are the following:

1. In Fern Hollow, Pittsburgh, a specimen was found in a stagnant pool, 6 to

10 inches deep, in yellowish brown mud. Its color was entirely yellowish brown, mottled lighter and darker, and no trace of olive-green was present. This apparently was a stray specimen.

2. A large male of the first form was found at Dunbar, Fayette County, the ground-color of which was salmon-color (VII, 17), the abdomen buff (V, 13), whitish on the sides. The red was brightest on the chelæ, with traces of green between the tubercles of the hand, and the lower side of the chelæ and body were dirty brown-ish yellow. This is apparently a case of albinism.

IV. ECOLOGY AND GEOGRAPHICAL DISTRIBUTION.

A. Ecology.³¹

Satisfactory conclusions as to the relation of geographical distribution to the physical conditions of the country can only be expected, if we know all about the ecological laws governing the different species. With reference to the seven species of crawfishes present in Pennsylvania, we shall see that the ecological conditions are quite varied, and the single species behave very differently. Thus it is necessary to discuss these facts first, before we attempt to study the distribution.

Three main types of ecological conditions may be distinguished among our crawfishes. We possess species which generally live in the larger rivers; other species which favor the opposite extreme, preferring the groundwater, where it is not far from the surface, and appears in the shape of springs and swamps; and intermediate between these two conditions is a species which selects the smaller streams for its home. We may conveniently call these "the river species," "the mountain-stream species," and "the burrowing species."

1. The River Species.

Cambarus limosus, Cambarus propinquus, Cambarus obscurus.

Although principally living in the larger rivers of the state, these species are not entirely restricted to them, being able to live in any larger body of water, running or stagnant, providing it is permanent. Thus these forms, in some cases, go

³¹ "Ecology," the science of the "relation of organisms to external conditions," is the oldest term, created by Hæckel (⁴⁴ Oecologie," in "Generelle Morphologie der Organisme," 1866). The term "Bionomics," which is often used in its place, was first introduced by E. Ray Lankester (in the article: Zoölogy, in Eucyclopædia Britannica, 9th ed., 1888, p. 803), and subsequently, but independently, (as "Bionomie") by J. Walther (*Einleitung in die Geologie als historische Wissenschaft*" 1. Bionomie des Meeres, 1893, p. XX). The term "Oecologie" was revived chiefly by E. Warming, (Plantesamfund, Grundtræk af den oskologiske Plantegcografi, 1895). The term "Ethologie" introduced by F. Dahl (Verh. Ges. Naturf. & Ærzte, Bremen, LXIII, 2. 1891. p. 123) has a wider sense, including also what we here call "life-history."

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far up stream into the smaller tributaries of our rivers, sometimes almost to their sources. The only condition which stops them in an up-stream migration seems to be the character of the watercourse, which must not be too rapid and rough. This is a very important fact, and largely explains the absence of these species in the mountainous regions of the state. On the other hand, these species are by no means averse to quiet bodies of water, such as ponds and lakes, and although the parts of Pennsylvania where these species are found are singularly free from lakes, erawfishes are almost regularly found in them, and even in artificial ponds, reservoirs, etc. It has been observed that in ponds and lakes these species seem to thrive exceptionally well.

Among the three species belonging to this class, there are certain differences. Cumbarus limosus of the eastern part of Pennsylvania has its main abode in the quiet streams of the lowlands. It goes up stream for a certain distance, but rarely, and only under exceptional conditions, (see below), is it found in streams which are somewhat rough. Its center, at least for this state, is in the lower part of the Delaware River, where it is under the influence of the tides. Here it prefers the muddy banks, living among the water weeds, and congregates often in large numbers at the mouths of small streams tributary to the river. In fact the latter places are the most favored, since this species loves to hide under stones, and it is chiefly at the mouth of streams that stones are found in this part of the Delaware. Further up stream, beyond the reach of the tide in the Delaware, and in its tributaries (Neshaminy Creek, Schuylkill River, Brandywine Creek) and in the Susquehanna and Potomac drainages, this species is generally found hiding under stones, as was first reported by Abbott (1873, p. 80) with reference to the Delaware River at Trenton, N. J. But such is not the exclusive habitat of C. limosus. It is very often found in quiet ponds, in ditches or canals, where there are no stones to afford con-In these places it frequents patches of weeds (Vallisneria, etc.), often in cealment. considerable numbers. From such places (ditches of the Delaware meadows at Trenton) it was reported by Faxon (1885a, p. 88). C. limosus is generally found in very shallow water, but sometimes at a considerable depth. I captured a few specimens in a quict cove of the Delaware River at Penns Manor, Bucks County, at the woodwork of a pier, at a depth of from six to eight feet (Sept. 15, 1905), and frequently got numbers of it in creeks and canals (Schuylkill Canal, Manayunk; Delaware and Raritan Canal, Princeton), in the water weeds, at a depth of from two to four feet. Although this species loves to hide under stones, and although it scoops out the dirt under stones, it is by no means a burrowing species. The hollows made under stones are very insignificant, and I have never observed that it

makes holes in the banks of streams. Faxon (1885*a*, p. 89) reports that Mr. Uhler found this species near Cumberland, Md., in "holes in the bottom and sides of a canal," but whether these were made by the crawfish, or were cracks and joints between stones, remains doubtful. In the lowlands in Maryland this species, according to the same authority, is found under stones in rivers and creeks. We may say of *C. limosus* that it is of all the species of this state the one which most decidedly prefers the quieter water of large rivers, canals, and ponds; that it likes to hide under stones, but is not at all averse to muddy bottoms and masses of vegetation.

The latter trait distinguishes it from the species of the western rivers, Cambarus obscurus, which dislikes muddy bottoms (without stones) and vegetation. In fact, this is so general a rule, that it is vain to look for C. obscurus in any part of a river which has no stones. Only in rare and exceptional cases have I found it not hiding under stones, apparently being forced to do so by necessity. I observed this in two cases: in the Allegheny River at Larabee, McKean County, and the Shenango River at Linesville, Crawford County. In both cases the river runs through peaty soil (through the Pymatuning Swamp at Linesville), and it was only after a long search that the species was discovered, when I struck places where stones were lying in the water. But it was interesting to note that at both places the supply of stones was apparently not sufficient to accommodate all the specimens, and so a number of them had to be content with a shelter afforded by the peaty banks, where they had built short, horizontal holes, not more than a few inches long, close to the edge of the water. These holes are apparently only temporary, and are often abandoned and changed, since a number of them were seen on the banks above the present water level, which were built and inhabited at a previous higher stage of the river. C. obscurus does not love vegetation. The patches of Dianthera americana, so frequent in our rivers, do not harbour many crawfishes, although they are not entirely absent from them; but they do not hide under these plants and their roots, but under stones. They always scoop out a hollow under the stone selected, and bring out the mud and gravel, throwing up a small rubbish pile in front of the hole, which, however, is soon obliterated by the current. The crawfishes are easily found by noting these rubbish piles. They rarely go into deep water (possibly only in winter), but always are close to the banks in shallow water; but on the other hand they never go out of water. In the mountains of western Pennsylvania this species is generally absent, and it is apparently the roughness of the streams which causes its disappearance. The stones, under which it hides, must be rather permanent in their position, and must rest upon a bed of mud, sand, or gravel, to afford congenial

conditions. In the mountain streams the rocks are rolled over very frequently, not only at high stages of water, but also under ordinary conditions, and this apparently does not suit the tastes of this species, and may be even directly dangerous. Since the general direction of the migration of this species in western Pennsylvania was and is upstream, it is evident that falls and rapids in the mountain regions present effective barriers. In the ponds and lakes of western Pennsylvania, connected with the Ohio drainage, this species is very abundant, but here also it always selects stones under which to hide.

Cambarus propinquus is restricted to Lake Erie and the lake drainage. It lives in the tributaries of the lake, exactly under the same conditions as *C. obscurus*. In the lake itself it has been found on two occasions. Dr. D. A. Atkinson collected a number at Presque Isle in the bay, but particulars as to their habitat were not recorded. The only other specimen from the lake was collected by myself on the sandy and gravelly beach near Miles Grove, thrown out by the surf, but alive. It does not seem to be very abundant in the lake, or at any rate seems to favor only certain places, and we may presume that places with stones and rocks on the beach and not too much exposed to the surf are the proper localities in which to look for it.

Cambarus propinquus sanborni in Ohio and West Virginia is found under exactly the same ecological conditions as its representative forms in Pennsylvania.

Nothing was known hitherto as to the ecological habits of *C. obscurus* and *propinquus*, except the short notice of Hay (1896, p. 498), that in Indiana *C. propinquus* lives "in the smaller streams hiding under stones, concealed in short burrows along the banks, or resting quietly on the bottom."

2. The Mountain Stream Species: Cambarus bartoni.

Conspicuously differing from "the River Species," *Cambarus bartoni* favors the rough streams of the mountains, hills, and the uplands generally, and is absent from the large rivers. The size of the stream may vary. In fact it goes up to the very sources and is found in the springs. The amount of water may be very small. Indeed it is frequently found in streams which dry out superficially during the hot season. But in such cases water is always present at a certain depth. The varying and often scanty supply of water forces this species to accommodate itself to these conditions, and thus it has become to a certain extent a burrowing species. It always selects stones to hide under, and in larger streams with a permanent supply of water is satisfied to scoop out a hollow under the stone after the fashion of *C. obscurus*. But very often the burrows are more complex, consisting of a hole going

down to a depth of a foot or even more. These burrows are found along the banks of the streams, and the opening is often not in the water, but away from it, but rarely more than a few feet. The deepest burrows are found in late summer and fall, when the small streams are almost or entirely dry. Then necessity compels the crawfish to dig deep to reach the underground water. I have observed burrows eighteen inches deep in a vertical direction (see Plate XLI, Fig. 1). Under these conditions a considerable amount of dirt (mud, sand, gravel), is removed from the hole, and this is piled up in more or less regular mounds at the entrance of the hole, often assuming the shape of "chimneys," which may be fully equal in size to those of the typical chimney-builders. Here we see the origin of this habit. *C. bartoni* is not an habitual chimney-builder, but is content to hide under stones and to scoop out shallow holes when the stream has plenty of water. But when the supply of water becomes scant it has to dig down to reach it, and the burrows and mud-piles are the natural consequences of the attempt of the crawfish to accommodate itself to these peculiar conditions.

The manner in which the burrows are constructed, and the "purpose" of the chimneys will be discussed below when we come to consider the true burrowing species, and it may be remarked here, that everything said with reference to the latter holds good also for *C. bartoni*.

The roughness of a stream presents no obstacle to the presence of C. bartoni. Indeed, it prefers small streams which descend in cascades and fall from the hillsides, provided the rocks lying in them arc stationary enough. It goes to the very uppermost springs and is frequently found there associated with C. monongalensis or C. carolinus, and also may be found near C. diogenes. I have observed cases where C. bartoni occupied holes, which were apparently built by specimens of these other species, and am able to give the following instances. Digging for C. monongalensis at West Brownsville, Washington County, I found in a large and wide hole a female C. bartoni (with eggs). The individual was much too small for this hole. To all appearances an old (abandoned?) hole of C. monongalensis was here occupied by C. bartoni. Similar observations were made at Avonmore Station, Armstrong County, where in the swampy ground of the valley of Long Run a colony of C. diogenes was found, and several C. diogenes were taken. In two holes, however, a halfgrown specimen of C. bartoni was found, and again these holes were much too large for them. This place was about fifteen yards distant from the stream in which C. bartoni was abundant. Another similar case was observed at Creekside, Indiana County.

Going down stream C. bartoni remains abundant, as long as the character of the
stream is maintained; after that it becomes scarce, but it does not disappear entirely, and in western Pennsylvania is frequently found associated with C. obscurus, in eastern Pennsylvania with C. limosus. In the large rivers it is generally entirely absent, and, if found, it is at the mouth of small streams, or at places where there are springs on the banks. Here it becomes evident that temperature plays an important part. The mountain streams, which are the favorite haunts of C. bartoni, are characterized all the year round by a rather uniform, but comparatively low temperature. In winter the temperature of the water goes down to just above the freezing point, but generally remains slightly higher (in running water about 35°-40° F.); in summer the maximum of these streams rarely goes above 60°, and does so only temporarily for a few days, while in the larger streams it remains for weeks above 70°, and may go up to 80° or even more. (The temperature of the Ohio River at Baden, Beaver County, on August 26, 1905, was 78° F. on a comparatively eool day.) That it is temperature which affects distribution is evident in summer, when in western Pennsylvania in the warm water of the rivers C. obscurus is found, but where there are springs on the banks discharging perceptibly eooler water into the river, C. bartoni suddenly appears.

It may be mentioned that I once found this species under very peeuliar conditions. At New Hagerstown, Carroll County, Ohio, I discovered numerous burrows in the black muck of a swampy meadow at the bottom of a small valley, which I took first for burrows of *C. diogenes*. But I was unable to get any *diogenes*, every hole investigated being occupied by *C. bartoni* (about half a dozen were taken). This part of the meadow was elose to a hillside, at the foot of which were numerous springs with a few stones, also sheltering specimens of *C. bartoni*. On the other side of the valley, which was about 100 to 200 feet wide, was a small stream with sandy and gravelly bottom, and a few stones, where also a few *C. bartoni* were present. The largest number of specimens was present in the swampy meadow, which is rather exceptional, but finds its explanation in the scareity of stones in this locality.

The variety *C. bartoni robustus* in general agrees with the typical form as eoncerns ecological conditions, especially in that it prefers rough, rocky streams.^{*} However, it was found preferably in streams of a larger size, avoiding the smaller headwaters. As Williamson (1901, p. 11) puts it: "at the headwaters" (Squaw Run, Allegheny County, is taken as an instance) "*bartoni* is found; following down the stream *robustus* is noticed; then an occasional *obscurus*; till finally *bartoni* becomes rare and disappears; then *robustus* disappears; and further down *C. obscurus* is the only species."

Since those parts of the stream which arc inhabited by *C. bartoni robustus* are always well supplied with water, this form does not need to make extensive burrows, and I have never observed regular chimneys.³²

The ecological conditions under which *C. bartoni* occurs were to some extent previously known. Goodman (1833 (1842), p. 293) gives a good account of them ³³ as observed in small streams near Philadelphia. According to Abbott (1873) it is found near Trenton, N. J., burrowing in the muddy banks of ditches and small streams, rarely of the river (Delaware). This, however, is not the usual condition, as we have seen above. Faxon (1885*a*, p. 63) says that it prefers cooler waters of mountain regions or uplands, living under the stones in clear streams and in springs, which is the usual condition under which it is found in this state. However, that there are variations in its habitat, occasioned by exceptional conditions, is seen from the case mentioned above from the state of Ohio, from Abbott's account, and from the observations of Dr. J. Sloan as reported by Faxon (*l. c.*), according to which, in southern Indiana, it is found in ponds and still water, not in running streams. This is, however, not always the case in Indiana, since, according to Hay (1896, p. 489) it is found in "springs and streams of clear running water, where it hides under stones or digs short burrows into the banks."

3. The Burrowing Species.

Cambarus carolinus, Cambarus monongalensis, Cambarus diogenes.

a. General habitat.

The burrowing species are always found at a certain distance from open water, although often in close proximity to streams, ditches, or ponds; but never, under normal conditions, *in* them. Exceptions are very rare, and only accidental, and found chiefly in the case of young individuals which have not settled down permanently, or of individuals which have been disturbed.³⁴ These species, however, always depend on the presence of water, but it is the groundwater which is inhabited

³³ The crawfish hole, eight to ten inches deep, with a wider chamber at the end, under stones in a small stream, with the opening in the water, undoubtedly belongs to this species.

³¹A case where young specimens of *C. diogenes* were found in numbers in open water by Dr. D. A. Atkinson will be discussed below. (See V.) This case is also to be regarded as exceptional.

³²Shufeldt (1896, p. 27) figures a chimney of *C. bartoni robustus* from near Washington, D. C. Why Shufeldt attributes this chimney to this form, I do not understand. He says that he studied burrows near Washington, "many of these were of *C. diagenes*, others were of *C. bartoni robustus*, which I found abundant in Montgomery County, Md." The specimen which built the chimney figured was not taken by Shufeldt, and he says that in the vicinity another burrow was opened which contained a *C. diagenes*. According to the description of the hole belonging to the chimney, it is too deep and complex to belong to *C. bartoni*, and I do not see any reason for not regarding it as belonging to *C. diagenes*.

by them, and thus they are found at places where the groundwater is near the surface, in springs and swamps. In order to reach the water these species have to dig a hole in the ground, which often goes down through a considerable amount of dry soil, but it is always filled with water at the bottom.

The three species belonging to this class differ slightly with regard to the selection of their localities. C. carolinus chooses the mountains, and is found in springy places on the highest parts of the Alleghany plateau. The most favored localities are high valleys with a "hard pan," that is to say a layer of stiff clay below, which serves to keep the groundwater within a few feet of the surface. In such places the surface is often apparently dry, but upon digging down fresh and clear spring-water is found at a depth of one to three feet, and the holes of this species go down to the "hard pan" in order to reach the water. C. monongalensis favors similar conditions, yet it does not live in the mountains, but on the foothills west of the Chestnut Ridge. (The physiographic classification of these features will be discussed below). In this region extensive valleys with clay bottoms are rarely found, and thus C. monongalensis is content with the more restricted deposits of clay found on the hillsides. Such localities, however, are very abundant in this region, and wherever there is a spring and a certain amount of clay this species occurs. It prefers the cool spring-water, and if the springs collect to form a small swamp, this species is found on its upper margin, not in the swamp.

C. diogenes does not haunt springs to the same extent as C. carolinus and C. monongalensis. It is sometimes found under similar conditions as the other two species, but generally at places where a spring or small stream spreads out to form a swamp. It is also abundant in swampy ground along the borders of ditches and streams, and in swamps formed in depressions of the valleys of the large rivers (abandoned ox-bows). In the formerly glaciated area of the state it prefers kettleholes. Like C. monongalensis it rarely occurs in the soft mud of swamps, but generally along their borders, where the firmer ground affords a better chance to dig more permanent holes. In consequence of the habit of preferring swamps to springs, C. diogenes is generally found at a lower elevation than C. carolinus and monongalensis, where it comes into contact with them. The two last named forms occupy the region of the clear and cool spring-water, while C. diogenes appears a little further down stream, where the water is not so clear, and in summer not so cool. In and near swamps the water in the holes of C. diogenes is often stagnant and muddy (even sewage is not much objected to by this species), while in the holes of the other two species there is always fresh and elear spring-water bubbling up.

b. Shape of the burrows. (See Pl. XL, Figs. 8 and 9, Pl. XLI.)

The burrows of these species (and also of *C. bartoni*) are to a certain degree alike, although they are very variable in depth and shape, so that there is very little uniformity. Only a few features are common to them. From the more or less dry surface they go down to the groundwater, where there is generally a kind of a pocket or widened chamber (Pl. XLI, Figs. 5 and 6). The width of the hole corresponds to the size of its inhabitants. It seems that one and the same individual permanently uses the same hole, although one and the same hole may be occupied by different individuals in succession, for an old abandoned hole may be occupied by a young specimen. This happens chiefly in localities where the holes are much crowded. There are places where the ground is fairly honeycombed with them,³⁵ and under such conditions a new hole may interfere with an old one, when a young specimen after attaining the proper size begins to build its own burrow, as it invariably does. If the old hole is abandoned the young specimen may take advantage of it, while in the alternative case, a fight ensues which ends in the expulsion or destruction of the weaker.

Each hole is always occupied by *one* individual only, with two exceptions. The first is the case of mating couples, when one adult male of the first form and one female are found in one and the same hole. The second is when the young of a certain size are associated with the mother in the hole of the latter.

The holes have all manner of shapes (see Pl. XL, and Pl. XLI). They may consist of a single shaft only, or may be more complex, branching off in various directions, and may have more than one opening at the surface. The chamber may be well marked or indistinct, and there may be several chambers. The chambers may be simple widenings of the hole, or may form side pockets. The direction of the descending shaft is rarely more or less vertical, and if vertical in the upper part, it generally soon assumes a slanting direction, and sometimes it is irregularly spiral. Shorter or longer branches may go off at the sides, and these may end blindly or may ascend to the surface. At the bottom side-branches may be absent, or may be developed to a considerable extent, running either horizontally or vertically. On steep hillsides, or along the banks of ditches, the general direction of the burrows is very often horizontal, the outward opening being lateral (Pl. XLI, Figs. 2, 3, 7).

The depth of the holes depends on the distance of the level of the groundwater

³⁵ I have seen this on the largest scale in the case of *C. carolinus* in the valley of Upper Decker's Creek near Reedsville, Preston County, W. Va. The whole valley, for two or three miles, offers favorable conditions for this species, and thousands of chimneys may be seen everywhere, coming up even between the railroad ties of the Morgantown & Kingwood Railroad.

from the surface. The holes are driven down by the crawfish to such a depth that a good supply of water is at the bottom at all seasons. Where the water appears at the surface, or is very near to it, the holes are sometimes hardly a foot deep. Generally they are considerably deeper, as much as two and three feet. They certainly at times go even deeper than this, but I never tried to dig at places where such conditions prevailed, that is to say, where from all appearances the level of the groundwater was more than three feet from the surface. Such conditions were not infrequently met with in the case of *C. carolinus*.

In a general way we may say that the holes of *C. bartoni* are very simple (Pl. XL, Fig. 8; Pl. XLI, Fig. 1). Among the true chimney-builders the holes of *C. diogenes* are also rather simple, consisting often of a single shaft with a pocket at the bottom (Pl. XLI, Figs. 5 and 6). In *C. monongalensis* they are decidedly more complex (Pl. XLI, Fig. 2), and the highest degree of complexity is reached in *C. carolinus* (Pl. XL, Fig. 9).

The shape of the burrows of *C. diogenes* was first described by Girard (1852, p. 89), who called attention to their variable character. Tarr (1884, p. 127) has given sketches of burrows of this species, and also observed their variability. Of *C. carolinus*, only the fact that it is a chimney-builder was known (Faxon, 1885*a*, p. 71). The burrows of *C. monongalensis* (as *dubius*) were described by Williamson (1901, p. 12), and he emphasizes their complexity as compared with those of *C. diogenes*.

c. Construction of the burrows and of the chimneys.

Although the "chimneys" or mud-piles at the mouths of the burrows have often been described and their purpose discussed, (Girard, 1852; Tarr, 1854; Shufeldt, 1896; Harris, 1903), the manner in which the crawfish excavates the burrow and piles up the mud in front of it had never been correctly observed. Abbott (1885) describes how Mr. J. DeB. Abbott saw the crawfish (*C. diogenes*) engaged in building its chimney, and states that it comes out of its hole "bearing on the back of its right claw a ball of clay mud, which by a dexterous tilt of the claw was placed on the rim of the chimney." This description, as we shall presently see, is apparently founded upon correct observation, but the observer witnessed only the final act, and drew from it a wrong inference. The old observation of Goodman (1833, (1842), p. 293), that *C. bartoni* brings out of its hole an "armful of rubbish and throws it over the side of his cell, and down the stream," should be quoted, since, although referring to another species, it is pertinent and applies well to the regular chimney-builders as regards the mode of carrying the mud.³⁶

³⁵ The way of carrying the mud out of the holes seems to be identical in all burrowing species. It has been observed in a similar form by Mr. W. S. Sutton in *C. pilosus* Hay, as described by Harris (1900, p. 272). That the crawfish uses

I have repeatedly observed the digging and the removal of the dirt out of the burrow. Of course it is impossible to see the digging going on in the field inside of the burrow, and consequently this was observed in the laboratory in the case of specimens of *C. diogenes* and *monongalensis* kept in captivity in large glass jars partly filled with clay and water. It is not difficult at all to see them at work, and after they have been brought into the laboratory the specimens begin to work within a short time, digging out the mud, carrying it upward and plastering it all over the walls of the jar. After some time (days or weeks), their activity lessens, and not much digging is done, producing the impression that they have become discouraged in the effort to construct something similar to the burrows in the field.

In digging the chelæ of the first pereiopods are used. The fingers are slightly spread out, so that they are about parallel, thus acting as forks for digging. They are pushed vertically down into the mud on both sides at the same time, and a lump of mud is thus loosened and lifted upward toward the ventral face of the body. In lifting the chelipeds are bent toward the body (the region of the mouth), and finally the ball of mud is appressed to the anterior part of the body and held in position by the chelæ. Very likely also the third maxillipeds take hold of it, but it was impossible to ascertain this. In this position, as Goodman expresses it, carrying an "armful" of dirt (or rather two armfuls), the crawfish walks slowly and deliberately to the mouth of the hole. I have repeatedly observed it coming out in nature.³⁷ It advances to the top of the chimney and deposits the mud pellet upon the rim, finally pushing it into the proper position with the upper (outer) surface of the claws. This latter act apparently was seen by Mr. J. DeB. Abbott; but according to my experience the mud is not brought up upon the back of the claw, but held, as described above, between the folded claws and the anterior part of the body.

After having been disturbed in the field, the crawfishes often begin to work again within a short time, and it is chiefly on such occasions that 1 have seem them at work, with the exception of one case, when I saw a large male of *C. diogenes* at work on the evening of April 30, 1905, (Sunday), in Nine-Mile Run, Pittsburgh. The

the "lateral tail-fins and telson" in any way, as suspected by Shufeldt (1896), in the sealing up of the orifice of the burrow, is hardly possible.

³⁷ The following particular instances may he mentioned: *C. bartoni* in a spring near Burgettstowu, Washington County, Aug. 4, 1904; *C. carolinus* at Indiau Creek, Fayette County, July 11, 1904; at Ohiopyle, Fayette County, July 12, 1904; at Myersdale, Somerset County, August 11, 1904; *C. monongalensis* in Fern Hollow, Pittsburgh, May 6, 1904; at Edgewood Park, Allegheny Connty, May 9 and 21, 1904; April 21, 1905; Monaca, Beaver County, June 30, 1904; at Cheat Haven, Fayette Connty, September 6, 1904; at Cameron, Marshall County, W. Va., May 1, 1905; at Morgantown, W. V., May 16, 1905; *C. diogenes* at Dunbar, Fayette County, September 7, 1904; iu Nine-Mile Ruu, Pittsburgh, April 30, 1905.

usual time for working seems to be at night, and I have repeatedly observed that holes and chimneys disturbed or destroyed on one day exhibited signs of recent action on the following day. The crawfishes also seem to work occasionally on rainy or cloudy days; at all events, on such days it is easier to induce them to come to the mouth of the hole.

As to the purpose of the "chimneys," different opinions have been expressed. Abbott (1884) believes that the chimneys are designed, and that the crawfish intends to build just such structures, that is to say, rather regular subconical mud towers. He maintains this against Tarr's view (1884, p. 127), that the chimneys are not a necessary part of the burrows, and that they simply are the result of the digging. Subsequent writers have rather inclined towards Tarr's idea, for instance Shufeldt (1896, p. 89), who says that it is easier for the crawfish to build a chimney than to carry the mud away from the hole, and that "it is the most convenient and safest way to get rid of the pellets, besides being the least troublesome, and the method by which they are the least likely to roll back into the burrow." Harris (1903, p. 605) thinks that the chimneys very likely are only "the result of the easiest method of disposing of the material removed in excavating the burrow."

I must indorse the latter opinion, and for the following reasons. Regular chimneys, although claimed by Harris (l. c.) to be "usually" present and well built, are by no means so frequent as believed by most authors. Of course they are abundant in each colony of chimney-builders, and attract the attention of the observer. However, according to my experience well built chimneys are rather scarce compared with the total number of holes existing in a particular locality. In the majority of cases only more or less irregular and shapeless mud-piles are found at the mouths of the holes, and it is only under certain favorable conditions that they assume the shape of "chimneys." These conditions occur when the upper part of the hole is more or less vertical (see Pl. XL, Fig. 9 at A; Pl. XLI, Fig. 2 at C; Figs. 7 and 8), so that there is opportunity for the crawfish, in bringing up the pellets of mud, to deposit them rather uniformly all around the rim of the chimney. Supposing that it is always the lowest part of the rim at which additional pellets are deposited, which is altogether a very likely supposition, if the crawfish wants to get rid of the pellets as quickly as possible, the chimney must grow regularly. If, however, the mouth of the burrow opens in a slanting direction or horizontally, more or less one-sided mud-piles will be the result. (See Pl. XLI, Fig. 2 at A; Figs. 3 and 4). Further, much depends on the character of the material brought up. If it is fresh clay (not disturbed before), as will generally be the case when the crawfish is digging out a new hole, the pellets will be firmer, stick better to the rim of the chim-

ney, and will remain in position, thus favoring the construction of a "well-built" chimney. On the other hand, when the mud is very soft, chiefly so when the crawfish is not digging new holes, but only cleaning out the old ones, the pellets are not firm, and the more liquid mud will flow down the outside of the chimney and render it lower and broader and, consequently, less "well-built." This latter fact also explains why young specimens often construct the neatest and most elaborate chimneys (Abbott). Young specimens, when they begin to work, bring out undisturbed, firm, and sticky clay, and the pellets are more likely to remain where they are placed on the rim of the chimney, which thus becomes very regular. Old specimens, on the contrary, live in holes which are practically finished, and when they work it is rather a process of "housecleaning" than of "housebuilding." The mud removed is more liquid and less sticky, and thus the chimneys are shapeless and irregular.

Very often the opening of the chimney is found closed. Abbott believes that the closing is merely the result of the accidental falling in of the rim. This may indeed happen, but in other cases it is plain that the crawfish closes the aperture intentionally, and Girard (1852) regarded this as the completion of the work of chimney-building. Shufeldt and Harris likewise believe that the crawfish itself seals up the burrow. This is my own opinion, and with Girard I think that the sealing up is the final act characterizing the completion of the burrow. Sealed burrows are very often found (see Pl. XL, Fig. 9; Pl. XLI, Figs. 2, 3, 4), chiefly in summer and fall, and it is in many cases evident, by the material used (see Pl. XLI, Fig. 6) that the shutting up was done by the crawfish by depositing pellets in the orifice. Often the "stopper" is not at the orifice itself, but a certain distance (5 to 6 inches) below. In fall the stopper is made rather substantially and fills the upper end of the hole for a distance of 6 to 10 inches (see Pl. XL, Fig. 9b at D), and such a filling cannot be accounted for by accidental falling in.

In my opinion the construction of the hole is the chief aim for which the crawfish works. For the removal of the clay and dirt an opening on the surface is needed; but when the burrow is completed this opening is shut up again, and the crawfish is content to remain inside, possibly for weeks or even months. This affords protection for the crawfish and its young from enemies (snakes). Females with eggs or young are almost always found in closed holes. It also affords necessary quiet and seclusion during the moulting process (soft shells are generally found in closed holes). It furthermore protects the hole from the disturbing influences of rain and frost. Of course it would not be advantageous to have the hole permanently sealed, since the crawfish wants to get out now and then (for mating, for

food), but this is necessary only at long intervals (even for food it is not absolutely imperative to go out frequently, see infra), and the stopper is easily removed. During winter a more effective stopper is provided by the crawfish, and it remains for three or four months shut up in its hole.

The chief activity in chimney-building is in spring.³⁸ During winter frost destroys or damages the upper parts of the hole, and the rebuilding necessitates a good deal of work, and large mud-piles are accumulated in consequence (4 to 12 inches high, 12 to 18 inches in diameter). But after the hole has been restored to a satisfactory condition work ceases, and in summer not much fresh mud is brought out. Occasionally new chimneys are seen in summer, and the activity may be resumed at any time if necessary. Besides young specimens remain active all through the summer. In *C. diogencs*, as we shall see, it is chiefly in midsummer that the young begin to build their own holes. In the other species this may take place at any time from spring to fall, and thus the new and often very regular chimneys of small specimens may be seen at any time during the warm season.

General activity again begins with older specimens late in the fall, and this has a very interesting cause, and my attention was called to it by Mr. F. E. Kelly of Pittsburgh, but I have confirmed it by subsequent observations of my own. It is evident that the deepest parts of the holes are occupied and used by the crawfishes only in winter; these parts go down to about three feet, and thus are entirely out of reach of the frost. In summer these parts are abandoned and the crawfish inhabits only the upper parts of its burrow. In digging for crawfish in summer I often followed the main hole to a considerable depth, finally discovering that this hole was filled with soft ooze and mud, and that no crawfish was in this part; further careful investigation generally revealed a side branch at a higher level, which was clear of mud, and here the crawfish was captured. In the fall the deeper, abandoned part of the hole (see Pl. XLI, Fig. 7 at c), which fills up during the summer with dirt, forming at the bottom of the hole a soft, pulpy mass, is reclaimed by the crawfish in order to go deeper down out of reach of frost; the mud is consequently removed, and the necessity of cleaning out these deeper parts of the hole is the cause of the renewed activity in the autumn (Pl. XLI, Fig. 7). Before Mr. Kelly communicated to me his discovery of this fact I had not paid attention to it, but was able to verify it in the summer and fall of 1905. The fall activity takes place

³⁸ Young specimens begin first, as soon as the frost is out of the ground. New chimneys of *C. diogenes* were seen on March 23, 1905, in Nine-Mile Run, and the activity was general on April 6, 1905, (Renfrew). The first signs of new chimneys of *C. monongalensis* were seen at Edgewood Park on March 18, 1905 (frost only partly out of the ground); the activity was general on March 31, (Colliers, W. Va.), and April 4 (Edgwood Park).

in the month of November (in the neighborhood of Pittsburgh), after the first killing frosts.³⁹

It is evident from the foregoing observations and considerations that the "chimneys" are not necessary parts of the burrows. They are simply the result of the work of the crawfish, and only represent the material removed from the holes, which must be carried somewhere, and is most conveniently disposed of right at and around the mouth of the hole. The regular shape of the chimneys is simply due to the way the crawfish has to work under certain conditions, and to the physical properties of the clay.

Nevertheless there are certain advantages connected with the shape of the chimneys, which, however, are by no means always present, and, in my opinion, are not originally intended. The uppermost part of the hole generally has the tendency to be more or less vertical; an addition of 4 to 12 inches adds so much to the length of the vertical canal, and the crawfish, when sitting at or near the mouth, is able to suddenly drop down to escape enemies, which, as I have repeatedly observed, it actually does. Thus a considerable length of the vertical part is decidedly advantageous, giving the crawfish a chance to get more suddenly and effectually out of reach of danger.

Another effect of the mud-pile is noticed when the hole opens horizontally on sloping ground (banks of ditches). Here the mud-pile generally is semicircular, convex toward the ditch, concave toward the mouth of the hole, and thus serves to keep the water at a uniform level in the hole (Pl. XLI, Figs. 2 and 3), for generally in such cases the hole has spring-water flowing out of it. This may be advantageous under certain conditions, since I have often found that by removing a pile of mud of this character I was able to drain off the water from a considerable part of the hole, thus making it distinctly uncomfortable for the crawfish, as is evidenced by the fact that it often came out of the hole, as if to investigate the cause of the sudden disappearance of the water.

³⁹ In 1905 it began rather late. On November 8, in Fern Hollow and Nine-Mile Rnn, no fresh chimneys were seen on the golf links, where *C. diogenes* is abundant. On November 22 fresh mud-piles were numerous at the identical locality, several sharp frosts having occurred in the meantime. The same dates and the same facts were ascertained for *C. monongalensis* in Fern Hollow. Mr. Kelly's observations were made November 14 and 15, 1904, but in 1904 I noticed fall activity as early as November 5 (Nine-Mile Run, *C. diogenes*). (See Pl. XLI, Fig. 5.)

B. GEOGRAPHICAL DISTRIBUTION.

(Plates XLII and XLIII.)

1. Cambarus limosus.

a. Summary of Facts (see above, pp. 356-358).

This species belongs to the rivers, ponds, and canals of the lowlands of the Atlantic Coastal Plain and the Piedmont region ⁴⁰ in the states of New Jersey, Pennsylvania, Maryland, District of Columbia, and Virginia. It has not been reported from the State of Delaware, but must certainly occur there also.

In Pennsylvania it extends up the rivers to a certain distance and in the Susquehanna River enters the Alleghany Mountain region. In Maryland it goes up the Potomae River, reaching the eastern extremity of West Virginia, thus also entering the Alleghany Mountain region.

Thus it is found in Pennsylvania in the drainages of the Delaware, Susquehanna and Potomac Rivers; but it deeidedly prefers the region of the lower Delaware, from the bend of the river at Trenton downward. Here it is exceedingly abundant, as also in the lower and quieter parts of the Schuylkill River at Philadelphia. It goes up the Delaware and Schuylkill, and is found in their tributaries within the Piedmont region, but here it is by no means as abundant as in the Delaware. It seems to be absent in the great Alleghany Valley between the Susquehanna and the Delaware, but reaches the foot of the Blue Mountain between the Susquehanna and Potomae, occupying the Cumberland Valley (part of the great Alleghany Valley), and in the Susquehanna and Juniata it ascends even further, far into the Alleghany Mountains (Center and Bedford Counties).

b. Origin of the distribution of C. limosus.

In Pennsylvania.

In the Delaware River above Trenton this species goes up as far as New Hope in Bucks County; but is very rare there, (only one specimen was secured by the writer after a prolonged search), and it seems that it does not go far beyond this point, if at all. Professor A. E. Davison informs me that it is not found near Easton, Northampton County, about ten to fifteen miles from the Blue Mountain, and I was unable to find it in the Little Lehigh Creek near Emaus, Lehigh County.

⁴⁰ As to the division of Pennsylvania into Coastal Plain, Piedmont Plateau, Great Alleghany Valley, Alleghany Mountains and Alleghany Plateau, see Davis, 1889, p. 187, and Hollister, 1904, p. 10, map, Fig. 1; also Powell, 1896, p. 73 et seq. and map, and Willis, 1896, p. 169.

Mr. W. R. McConnell mentions (in his notes) the absence of crawfish in the Delaware at Portland, Northampton County.

It is found, however, in small tributaries of the Delaware in the southeastern half of Bucks County (Neshaminy Creek). In the Schuylkill River it goes up to Reading (Girard and also McConnell), and slightly beyond (Maiden Creek) in Berks County, but I have not been able to find it in the Schuylkill, where it comes out of the Blue Mountain, (Shoemakersville). It has been reported from Brandywine Creek in Chester County.

It is known from a number of places in the drainage of the Susquehanna, but they are all in the region of the Great Alleghany Valley or the Alleghany Mountains. I was unable to find it in the Susquehanna in Lancaster and York Counties, (Pequea and York Furnace), and I do not think that it is present there on account of the roughness of the river, which flows over a rocky bed in a channel cut deep into strata, chiefly of the archaic age, belonging to the Piedmont Plateau, from York Haven to the Maryland state-line and beyond. Such conditions are decidedly unfavorable for this species, and it is rather strange that it should be found at all above this rough part of the Susquehanna, which is about thirty to forty miles long. I think that this species immigrated into these parts in very recent times by way of the Susquehanna and Pennsylvania canals, which closely followed the river from its mouth in Maryland to the New York state-line and the Juniata up to Hollidaysburg, and connected it with the Schuylkill. These canals were maintained and in use a long time, beginning as early as 1834, were abandoned about 1890,⁴¹ and at present only remnants of them are seen. C. limosus is often found in canals. First reported by Faxon from near Cumberland, Maryland, I have found it in considerable numbers in the Schuylkill and Delaware and Raritan Canals. It is quite possible that the Susquehanna and Pennsylvania Canals afforded this species the means of reaching the Susquehanna River in the region of the Great Alleghany Valley south of Harrisburg. Its further distribution up stream is then not strange, after the rough portion of the lower Susquehanna had been overcome, or avoided.

The same may be true of the Schuylkill River. Although certainly originally present in the lower part, it was the Schuylkill canal (once connected with the Penn-sylvania canal) which possibly afforded an opportunity for *C. limosus* to go up the river as far as it does now, since the Schuylkill above Philadelphia is rather rough.

⁴¹ The main line of the canal was completed in 1834, the Susquehanna Canal from Columbia to Havre de Grace in 1840; see Jenkins, 1903, pp. 275, 277, 282 and Klein, 1900, p. LXXIX; see also Hoyt & Anderson, 1905, p. 24. In the latter paper fine views of the scenery of the lower Susquehanna are published (Pl. 1, B, Pl. 8), which convey a good idea of the roughness of the water of the river.

Similar conditions seem to have played a part in the distribution of this species in the Potomae River. It has been reported from an old canal (Chesapeake and Ohio) four miles south of Cumberland, and I have found it in the Potomae at Cherry Run, West Virginia, and at South Cumberland. At both places it was searce, and I am much inclined to believe that in this region (western Maryland and castern West Virginia) it got into the river from the canal. Originally its distribution in Maryland was very likely similar to that in Pennsylvania, belonging only to the Coastal Plain and the Piedmont Plateau.⁴²

Of the tributaries of the Potomae in southern Pennsylvania those which empty into the Potomae east of the Alleghany Mountain region also possess this species. It has been found in the drainage of the Monoeaey River at Gettysburg, Adams County, and that of the Conocoeheague Creek in Franklin County, the latter locality again belonging to the Great Alleghany Valley. Further west, within the Alleghany Mountains, it seems to be absent. I did not find it in Big Cove Creek and Tonoloway Creek, Fulton County, and it is not in the collections made by Mr. H. A. Pilsbry for the Philadelphia Academy in Sideling and Town Creeks, Washington and Alleghany Counties, Maryland. This supports the view that the presence of this species in the Potomae as far up as Cumberland is due to the existence of the canal. Above Cumberland, where the eanal ends, *C. limosus* is positively absent in the Potomac drainage in Pennsylvania as well as in Maryland and in West Virginia.

Thus it seems that *C. limosus* belongs originally only to the larger rivers of the southeastern section of our state, and that its real eenter for Pennsylvania is the Delaware. It has spread, however, upstream, and has approached the Alleghany Mountain region, even entering the latter in the Susquehanna River. This upstream dispersal is apparently not everywhere due to natural migration, but has been favored in recent times by canals. The present northwestern boundary, disregarding the Susquehanna River, is marked by a line (see Pl. XLIII) running from New Hope, Bueks County, to Maiden Creek and Reading, Berks County, thence to Bainbridge, Laneaster County, Carlisle, Cumberland County, and to Williamson, Franklin County. This line, generally speaking, runs parallel to the Blue Mountain, and it is very likely that the differences in the physical features of the Piedmont Plateau and the Alleghany Mountains have something to do with the distribution of this speeies, although the real cause cannot any longer be clearly seen, the original conditions being apparently obscured by several factors. For it should not be forgotten that the streams from the Susquehanna to the Delaware, issuing through the Blue

⁴² The Chesapeake and Ohio Canal forms a continuous waterway from Washington to Cumberland, and was completed in 1850, see Hulbert, 1904, p. 160, and map opposite p. 80.

Mountain from the Anthracite basin, are largely charged with mine-water, and in this section of the state (Berks and Bucks counties) we see that *C. limosus* does not so closely approach the Blue Mountain, while in Cumberland and Franklin Counties, where the streams are clear, it goes to the very foot of the mountain.

Of course we cannot any longer ascertain what the original conditions were, and thus it is hardly profitable to enter into any further speculations. It is probable that the original range of this species has been reduced on the one hand by pollution of the streams, and has been extended on the other hand by modern river improvements. How far this holds good in detail, remains doubtful.

General origin of the distribution of C. limosus.

Aside from the more recent dispersal of this species just discussed, we are prompted to inquire how this species was able originally to reach the parts where it is now found.

As the writer has pointed out in a former paper (1905b, p. 108, 111, 114, 127) C. limosus stands rather isolated geographically as well as morphologically. It belongs to an ancient group of the subgenus Faxonius, probably the most ancient, which consists of five species. The other four species are entirely removed geographically from C. limosus, and are found in the central basin of the United States, in Kentucky, Indiana, and Missouri, that is to say, about four hundred miles to the west of the range of C. limosus, with the Appalachian System between them. We have to deal here with a marked case of discontinuity of distribution in the limosusgroup. Since, as has been shown by the writer in the paper referred to, we locate the center of the subgenus Faxonius in the central part of the Mississippi drainage, C. limosus must have reached its present home by migration, and there are several ways by which it may have gone.

The most direct route is across the Alleghany Mountains. We may suppose that the *limosus*-group once extended in the Ohio drainage up into western Pennsylvania and West Virginia, and that it was able by some means to cross the divide into the Atlantic drainage. This does not appear impossible, inasmuch as in the mountains stream-piracy has taken place on a large scale during all ages (Davis, 1889). In fact all of the larger rivers now running into the Atlantic have captured large tracts originally belonging to the interior drainage, and the divide has been continuously shifted westward.

On the other hand, considering the ecological peculiarities of *C. limosus*, this assumption does not appear very likely. The habit of living in larger streams in rather quiet water would not favor a migration across the mountains, and if this

form actually came by the way indicated some traces of its former existence should have been left in Pennsylvania, Maryland, or the Virginias, chiefly since there was no competition by any other species, river-forms being absent in the Alleghany Mountain region. Thus the direct route across the mountains seems to be out of the question, and this is further rendered probable by another consideration.

C. limosus being ancient, its migration eastward must have taken place at a remote epoch, certainly at an earlier time than that of a group which is more advanced, namely, the propinguus-group. As we shall see below, the latter existed already in Preglacial times, and thus we are forced to place the origin of the *limosus*-group at least as far back as the Tertiary. During this time, however, the Ohio in its present form did not exist. There was Spencer River,⁴³ in West Virginia and western Pennsylvania, and another river (Old Kanawha)⁴⁴ in West Virginia and Ohio, running northward to the Erigan River, which transversed the basin of Lake Erie.⁴⁵ And further the present upper Susquehanna (North Branch) is apparently new. It must have taken in Preglacial times a northward route toward the St. Lawrence basin, possibly also to the Erigan River (White, 1896, p. 376). All these rivers flowing northward in Pennsylvania and Ohio were different in character from what the rivers of this region are now. Their fall was slight, and they were rather sluggish. This is positively known of the Spencer River (or the Old Monongahela), which must have been practically at base-level (White, 1896, p. 377). If this was the case, nothing is opposed to the assumption that C. limosus (or its ancestral form) once was an inhabitant of some of these rivers. But then we see that its eastward migration cannot have been in a direct route, but must have gone on in a roundabout way, chiefly by the old Erigan River.

If the Erigan River was tributary to the Mississippi system, this is easy to imagine. If it drained to the St. Lawrence Gulf, as Spencer believes, we must assume an earlier crossing of the continental divide by this form, wherever this was situated (Indiana?), and then again a crossing of the divide between the Erigan River and the Atlantic coast drainage.

Be this as it may, we are forced to move the old range of the *limosus*-group to the north, into the Erigan River drainage, and this gives us the means of explaining the discontinuous range of this group. If it were at one time present in an area extending from Kentucky and Indiana through Michigan into Ontario, and if we assume that it crossed over into the Atlantic drainage somewhere in northern Penn-

⁴³See Foshay, 1890, p. 368; Leverett, 1902, p. 89.

⁴⁵See White, 1896, p. 376; Leverett, 1902, p. 100; Tight, 1903, map, Plate I, Plates 16 and 17. (Teays River.) ⁴⁵See Spencer, 1881, map 2, and 1894, p. 293.

sylvania or New York, the advancing ice of the Glacial Period must have entirely eovered a large part of this range. In the central parts, in Ohio and western Pennsylvania, it was impossible for these forms to retreat southward, these parts being occupied by another vigorous group of river-erawfishes, as we shall see below (*propinquus*-group), and only in the cast and west a chance to survive was left. The eastern remnant is the present *C. limosus*, the western is the group of species found now in southern Indiana and Kentucky.

How C. limosus reached the Atlantic Coastal Plain from the Erigan basin is very hypothetical. One suggestion may be made. Not only does the North Branch of the Susquehanna seem to be a reversed river, but the West Branch has captured a large part of the original drainage of the Alleghany Plateau in Potter, Cameron, and Clearfield Counties. Davis (1889, p. 248) believes that this happened largely in Pretertiary times, since he thinks that the Alleghany Plateau belongs to the Cretaeeous peneplain. However, Campbell (1903, p. 280) has shown that there are two old base levels in northern Pennsylvania, an older one (Cretaeeous), identieal with that of Davis, and a younger one (1,600 to 2,200 feet) eorresponding to the Harrisburg peneplain of Old Tertiary age. Since the headwaters of the West Branch of the Susquehanna are earved into this second peneplain, it is probable that during Tertiary times the stream-piracy of the Susquehanna was going on rather vigorously. If we assume that C. limosus in Tertiary time existed in this part of the Erigan River drainage, namely in the Old Upper and Middle Alleghany Rivers,⁴⁶ which did not belong to the Old Monongahela or Speneer River, it must have been possible for it to get into the Susquehanna drainage in eonsequence of this stream-piracy in Tertiary times. This, however, is a mere suggestion. There is no other evidence for it but the bare fact that stream-piracy has gone on in this region. I mention it here only to show that the erossing over of this species into the Atlantie drainage is not altogether unthinkable.

After arriving in the coastal plain *C. limosus* was cut off in the Glacial Period from its allied forms in the west. But it survived, and in Postglaeial times was able to advance again. But the Postglaeial dispersal eannot have amounted to much, since the inereasing roughness of the streams, caused by the Postglaeial elevation of the eountry, was not favorable to a northward expansion. We do not know the exact northern boundary of *C. limosus* outside of our state. It is found in New Jersey as far north as Morris County, yet we do not know whether it reaches Raritan and New York Bays, and the Hudson River. No positive record from New York State is at hand (see De Kay, 1844, p. 23, and Paulmier, 1905, p. 117).

⁴⁵See : Carll, 1880, pp. 333 and 336, map, Pl. 2 ; Leverett, 1892, pp. 129 and 132 ; Tight, 1903, map, Pl. 1.

An alternative supposition might be entertained. *C. limosus* might have arrived in its present home coming from the south by way of the Atlantic Coastal Plain. This, however, does not seem probable. First of all, the distribution of *C. limosus* does not extend southward beyond Virginia, and even in Virginia it is known only from a few localities. Southward no representative of this group is known on the coastal plain, and, if *C. limosus* had come from the 'south, traces of this migration might be expected. On the other hand, if it came from the north, as we here assume, the fact that it did not spread beyond Virginia may be accounted for by the presence of another group of this genus, the subgenus *Cambarus* (*blandingi*-section), in the southern parts of the coastal plain, which, like *C. limosus*, prefers ponds and sluggish streams. Indeed both species (*C. limosus* and *C. blandingi*) are found actually associated at the same localities (by Faxon, 1885a, p. 88, at Trenton, New Jersey, and by the writer in the Delaware and Raritan Canal at Princeton, New Jersey), but we must bear in mind that in New Jersey, and also in Maryland and Virginia, *C. blandingi* is an intruder, its chief domain being in the Carolinas.

The following are conclusions from the above considerations:

Cambarus limosus is an ancient species, characterized by morphological and geographical isolation. The most closely related forms are found in Kentucky and southern Indiana. An attempt to explain the presence of C. limosus at its present location has to connect its range with that of these related species. A connection by way of the Atlantic Coastal Plain southward is out of the question. Thus only the connection across the Appalachian system remains. The fact that the rivers just west of the mountains in western Pennsylvania arc occupied by a more advanced group of species (propinguus-group) of a subgenus which is certainly of Preglacial age, as we shall see below, leads us to the conclusion that the limosusgroup also must be not only Preglacial, but older than the propinguus-group. But at that time there was no direct way from the lower Ohio, where its center of distribution was situated, into western Pennsylvania and across the mountains, the Ohio having no existence as yet, and the general drainage in this region being to the north. This leads us to assume a former more northern range of the limosusgroup, extending into Preglacial Canada; and this assumption furnishes an explanation why it was possible for the Glacial Epoch to cut the range of the limosusgroup in two, leaving no representative of it in the region now drained by the middle and upper Ohio. Cambarus limosus is a Tertiary type, and it reached its present area coming from the west and by way of the north, being driven south along the Atlantic Coastal Plain by the advancing iee of the Glacial Period. It survived during the Glacial Period in the region of the lower Delaware River and Chesapeake Bay, while

all the rest of the former range of the group was covered by ice and its representatives were destroyed, with the exception of a small remnant in the southwestern portion of the range, in southern Indiana and Kentucky, outside of the glaciated area. The reason why this group was destroyed in the glaciated area, and was not able to retreat southward and to survive in the intervening parts (Ohio, western Pennsylvania, and West Virginia), was that here the rivers were occupied by another group of the subgenus.

The above is a mere theory, and it remains doubtful by which way *C. limosus* reached the Atlantic Coastal Plain. The assumption that it was by way of the Erigan River and the St. Lawrence basin satisfactorily accounts for the facts, but this is the only point directly in favor it. However, the study of the distribution of *C. limosus* is not yet finished, since the actual boundaries of the distribution, chiefly to the north and south, are not positively known. But this does not concern us at present, since they are not situated in the State of Pennsylvania.

In C. limosus we have a species which survived during Glacial times in a part of the Atlantic Coastal Plain which is well to the north, not far from the southern edge of the ice. Of course this forms a part of Adams' (1902, p. 121) southeastern center in its widest sense, lying at its northeastern extremity. Although surviving not far from the edge of the ice, C. limosus cannot be considered as belonging to the tundral biota (Adams, 1905, p. 58), but it belongs very likely to the second wave (northeastern biota), with a slight suggestion of the third wave (southeastern biota) (l. c., pp. 58 and 62). As Adams indicates, the first and second waves of Postglacial dispersion had their glacial homes in very narrow belts parallel to the southern edge of the ice, while the southeastern (and southwestern) biota covered in Glacial times wide tracts of country. The second wave largely invaded the coniferous forest-belt of Canada, while the third wave was more stable and did not spread so far northward. With regard to its geographical location during Glacial times, C. limosus should be classed with the northeastern biota; and with regard to its stability in Postglacial times, with the southeastern. But we are to consider that a Postglacial northward dispersion was rendered difficult in this case by the physiographical features of the country. The coastal plain with its sluggish streams and stagnant ponds disappears in northern New Jersey, the uplands (Piedmont Plateau) reaching the coast in the vicinity of New York Bay (see McGee, 1888, Pl. 2); this did not offer advantageous conditions for this species, and thus it remained within comparatively narrow limits in a corner, into which it was pushed in Glacial time. C. limosus is a Tertiary relic at the northern extremity of the coastal plain, which has not been able to expand its area to any considerable degree in Postglacial times.

2. Cambarus propinquus, Cambarus propinquus sanborni and Cambarus obscurus.

a. Summary of Facts. (See pp. 362-363; 368-369; 372-373.)

If we desire to arrive at a proper understanding of the distribution of *C. propinquus, C. propinquus sanborni*, and *C. obscurus*, they must be discussed together.

The area occupied by these three forms (see Pl. XLII, Fig. 3) includes eastern Iowa, southern Wisconsin, northern Illinois, Indiana, Michigan, Ohio, northeastern Kentueky, northern West Virginia, western Pennsylvania, western New York, and parts of Canada (Ontario and Quebee). In the western and northern part of this range *C. propinquus* is found; *C. propinquus sanborni* oecupies the larger part of Ohio and parts of Kentucky and West Virginia; while *C. obscurus* has its chief domain in western Pennsylvania, passing southward into West Virginia and northward into New York. Thus it is apparent that the three forms oecupy different sections of the general area of the group, *propinquus* being western (and northern), *sanborni* central, and *obscurus* eastern. As far as observations go all three forms are rather [sharply separated geographically, although they come into contact at the edges of their ranges. This is especially true, as we have seen, in our state and the adjacent portions of Ohio and West Virginia, while in western Ohio and in Indiana nothing is known of the boundaries of the forms represented there.

In Pennsylvania only two of these forms are found (Pl. XLII, Fig. 2). *C. propinquus* is restricted to Lake Erie and its drainage; *C obscurus* belongs to the Ohio system, and is found everywhere in the western section of the state, in the Ohio, Monongahela, and Alleghany Rivers and their tributaries. The boundary toward the east is formed by the divide between the Alleghany and Susquehanna systems, and farther south generally by the Chestnut Ridge (with exceptions to be discussed below). Northward this species crosses over into the Genessee drainage, and extends into New York. It also erosses over into the Lake Erie drainage in Pennsylvania.

Along the western border of the state it passes beyond the state line into Ohio, the drainage belonging in the northern part to the Beaver River. Furthermore it goes down the Ohio and is found in all ereeks running from Pennsylvania through the Panhandle of West Virginia as far south as Fish Creek in Greene County, Pennsylvania, and Marshall County, West Virginia. Fish Creek falls into the Ohio a little below Moundsville, West Virginia, and contains only the typical form of *C. obscurus*.

Going further down the Ohio eonditions suddenly change. In Fishing Creek, Wetzel County, West Virginia, which empties into the Ohio near New Martinsville, about thirteen miles below the mouth of Fish Creek, *C. propinquus sanborni* appears. But the form here found is not typical. As we have seen above, it inclines some-

what toward *C. obscurus*, and one individual has been found which represents typical *C. obscurus*. In Middle Island Creek near St. Mary's, Pleasants County, West Virginia, which is about twenty-five miles further down the Ohio, the few specimens collected seem to be typical *C. propinguus sanborni*.

Thus it appears that *C. obscurus* goes down the Ohio River to about Moundsville, West Virginia. All the tributaries of the Ohio in the Panhandle possess this species, and very probably it will be found also in Ohio on the opposite side of the river. But crossing over the divide between this part of the Ohio and the Muskingum-Tuscarawas River in Ohio, we again find *C. propinquus sanborni* in the drainage of the latter. The western boundary of *C. obscurus* consequently is formed by the divide just mentioned, but this line crosses the Ohio River between Moundsville and New Martinsville, West Virginia (Pl. XLII, Fig. 2, and Pl. XLIII).

Further to the south in West Virginia in the drainage of the upper Monongahela this species has not been traced. It surely goes up the Monongahela beyond the southern boundary line of Pennsylvania, but how far has not been ascertained.

The fact that *C. obscurus* is found also in the Potomac drainage, in Wills Creek, between Hyndman, Bedford County, Pennsylvania, and Ellerslie, Alleghany County, Maryland, deserves special mention, and will be commented upon elsewhere.

b. Origin of the distribution of C. propinguus, propinguus sanborni, and C. obscurus.

In order to get a fair understanding of the distribution of these forms, we must take notice of the Preglacial physiography of the region in which they are found, for, as we shall see below, we are led to believe that these forms are of Preglacial age, and survived during the Glacial Period in the southern parts of the drainage systems, which now constitute that of the Ohio.

First of all, we should bear in mind that at the end of the Tertiary Period before the ice pressed down from the north, the Ohio River in its present form did not exist. In the whole region, drained now by the middle and upper Ohio, the drainage was at that time not to the west, but to the north, and it was collected by a river running in a northeasterly direction toward the present Gulf of St. Lawrence, (the Erigan River or Ancient Grand River).⁴⁷

Disregarding some smaller streams, for instance the Old Middle and Old Upper Alleghany, which do not concern us here, three main rivers, tributary to the Erigan River, have been traced with more or less accuracy, and the evidence for their existence, although fragmentary, leaves no doubt as to the general correctness of the

⁴⁷ This is the opinion of Spencer (1881 and 1894). Others believe that this river drained toward the Southwest, into the Mississippi; see Grabau, 1901, maps, p. 44 and 45 (Dundas River).

main features of this drainage, which differs so strikingly from that which exists to-day.

The easternmost of these rivers was the Spencer River, or Old Monongahela, or Old Upper Ohio,⁴⁸ which drained southwestern Pennsylvania, northern West Virginia, and a small part of eastern Ohio. West of it was the Old Kanawha River, or Old Middle Ohio, or Teays River (Leverett, 1902, p. 100, map, p. 101; Tight, 1903), which drained parts of West Virginia and Kentucky, and the larger part of central Ohio. The old Muskingum-Tuscarawas River belonged to this drainage, the Muskingum River not flowing southward, but westward and southwestward from near Zanesville, Ohio, to Circleville, Ohio, thus joining the Old Kanawha (Newark River; Tight, 1903, Pl. 1).

The divide of the Old Kanawha to the westward was formed by the Cincinnati uplift, and was situated according to Leverett (1902, p. 100) near Manchester, Ohio, on the present Ohio River. Beyond this divide we have the Lower Ohio system (Leverett, p. 109). The Preglacial lines of discharge in this region are rather obscure, but according to Leverett and Newsom (1902, p. 168, Pl. 6) it is probable that a large part of the present system of streams was tributary to the lower Ohio in Preglacial times, but that a small number of them may have had a northward discharge through the Great Miami basin in western Ohio (Leverett, p. 116). There are distinct indications of a northward drainage in the vicinity of Cincinnati (Cincinnati River, Tight, 1903, Pl. 1). This possibility is also admitted by Newsom (1902, p. 181).

We may take it for a well established fact that in Preglacial times at least two rivers existed in this region, the Spencer and the Old Kanawha, which did not drain into the Ohio and Mississippi in a southwestern direction, but flowed northward into the Erigan basin. Westward there was very likely a third river ("Old Miami") running in a similar direction; but in this region we arrive at the old Preglacial divide between the Lower Ohio and the Erigan River. It remains doubtful whether the latter drained to the St. Lawrence Gulf or to the Mississippi by the way of the present Wabash.

Assuming the theory of the former existence of an Old Miami (or Cincinnati) River, we see that there are certain interesting relations of these three old rivers to the present distribution of the three forms of *Cambarus* under discussion.

Of course, we must disregard those parts of the ranges of these forms which lie

⁴⁸ See above, p. 429. Descriptions are given by Foshay, 1890, White, 1893, and Leverett, 1902, p. 88 (with map on p. 89). Additional evidence has been furnished by Hice, 1903, p. 302. Another name is Pittshurgh River (Tight, 1903, Pl. 1).

in the formerly glaciated area, for these are due to Postglacial expansion. But looking upon the localities south of the terminal moraine (Pl. XLII, Fig. 3) we see that only a few are known for C. propinguus, and these are all in southern Indiana (Brown, Monroe, and Green Counties),⁴⁹ and belong very likely to the old Lower Ohio drainage, but in the region where it comes into contact with the supposed Old Miami River (or possibly some other river flowing north in the State of Indiana). Since we have reason to believe (Ortmann, 1905b, p. 114) that the center of radiation of the subgenus Faxonius, to which the propinguus-group belongs, is in the central basin formed by the three great rivers (Missouri, Mississippi, and Ohio), C. propinguus distinctly points toward this center, of which southern Indiana forms part. This is the more interesting since we see that it is the most primitive species of the propinguus-group which most closely approaches the original center. In Preglacial times C. propinguus belonged to the northeastern extremity of the old Ohio drainage (Lower Ohio), and in this region there apparently was a chance for it to cross over the continental divide into the Atlantic (St. Lawrence) drainage. If, however, the Erigan River drained to the Mississippi, the presence of this species in the Lower Ohio and in the lower part of the Erigan River is more easily accounted for by direct communication of the waters.

Taking up the distribution of *C. propinquus sanborni*, we observe that until recently only one locality was known to the south of the drift, namely, the type locality in Carter County, Kentucky, which is undoubtedly in the drainage of the Old Kanawha River. In addition, I have discovered a number of localities in eastern Ohio (Carroll, Harrison, and Stark Counties), and in northern West Virginia, which belong to the same drainage (Newark River and Marietta River, tributaries of the Old Kanawha), which are also outside of the glaciated area (at Canton, Stark County, Ohio, close to the edge of the drift).

The chorological facts about the distribution of *C. propinquus* and *C. propinquus* sanborni are very meager, and not at all satisfactory; but as far as our present knowledge goes, all known localities of *C. propinquus* sanborni, outside of the drift, are in the drainage of the Old Kanawha, while none of the known localities of *C.* propinquus are in this drainage, but are situated to the west of it. Now, this mutual relation between distribution and Preglacial drainage becomes more evident when we look upon *C. obscurus*, the distribution of which I have studied more closely.

⁴⁹ They are close to the southern edge of the drift, and it is a little doubtful whether they are inside or outside of it. Disregarding the Illinoisan drift, they are surely outside of the Postillinoisan glaciation, as is also a locality in Franklin County, Ind.

Leverett (1902, p. 89, Fig. 1) has given a map of the Old Monongahela River, which is reproduced on Plate XLII, Fig. 1, and alongside of it, Plate XLII, Fig. 2, I give a map of the present distribution of *C. obscurus*. It is evident at a glance that there is close correlation between *C. obscurus* and this old river. The most important features are furnished by the western boundary. The divide between the section of the Ohio which runs along the Panhandle of West Virginia and the Muskingum-Tuscarawas drainage is the old divide between the drainages of the Spencer River and the Old Kanawha. This divide crosses the present Ohio-just above New Martinsville (see Leverett's map, p. 90, Fig. 2: "probable early divide"). As I have found (p. 434) this old divide ecoineides with the present boundary between *C. obscurus and C. obscurus sanborni*. It also is significant that it is not the Tertiary (Preglacial) divide, which is located by Tight (1903, Pl. 11) just below New Martinsville, nor the "later divide" of Leverett (*l. c.*), but just the one which existed at the beginning of the Glacial Period. We shall have to return to this topic.

Thus it is clear, *first*, that the original separation of these two forms was brought about by the fact that they belonged to different river systems; *second*, that we must assume the Preglacial age of the *propinquus*-group; and *third*, that the distribution of these crawfishes furnishes additional evidence for the correctness of the view of the Old Monongahela and Old Kanawha, as held by Leverett (and others); and with reference to these crawfishes it seems to me that the following theory is rather well founded.

In Preglacial times, the propinques-group, coming from the southwest (lower Ohio) reached the Erigan River drainage (either directly or by erossing a divide), of which it became characteristic.⁵⁰ It entered, consequently, also the southern tributaries of this river, and owing to the fact that there were three main tributaries, this group developed the tendency to split up into as many geographical forms. These were apparently the conditions when the Glacial Period began.

The chief effect of the advancing ice was that the northern parts of the range of this group were covered by ice. Only in the region of the headwaters of these rivers, to the south of the edge of the ice, was there a chance to survive, and survival here occurred. Both the Old Monongahela and the Old Kanawha were

⁵⁰ We have seen that a similar dispersion very likely took place in the case of the *limosus*-group. The latter being more primitive, we must assume that it formed a first and earlier wave of immigration from the Lower Ohio into the Erigan drainage, while the *propinquus*-group came later. This movement is still going on. There is evidence of a subsequent Postglacial wave (later than the Postglacial migration of *C. propinquus*) also starting from the Lower Ohio, and represented by the *rusticus*-group, which again has all the morphological marks of a more recent type than the *propinquus*-group. But this is outside of the scope of the present paper.

dammed up by the ice, and transformed into lakes (Lake Monongahela of White, 1896, and Lake Ohio, cf. Jillson, 1893, p. 19, and Map, Pl. 5, with the necessary restrictions), and this led to the result that the colonies of crawfishes belonging to the southern (upper) parts of these rivers became sharply separated from each other, and I think that the tendency toward the formation of three species (C. propinquus, C. sanborni, C. obscurus) is directly due to this process and to physiographical conditions prevailing in the earlier part of the Glacial Period (Kansan or Prekansan, cf. Hice, 1903, p. 300).

Finally these lakes were connected and drained off toward the southwest, thus forming the present Ohio River (Postkansan, but before the Wisconsin stage, cf. Hice, 1903, p. 299); the areas of the three forms of crawfishes were reunited, but the different parts of the new Ohio drainage are occupied by different forms of the propinguus-group, remaining in their original areas; the upper Ohio is characterized by C. obscurus, the middle Ohio by C. propinguus sanborni, and the lower Ohio by C. propinguus.

But additional changes took place in Postglacial times. According to the present distribution these must have been greatest in the case of C. propinguus. Almost the entire range of this form lies within the glaciated area, and thus it is beyond question that its present distribution is largely due to the Postglacial migration northward and northeastward.⁵¹ This migration possibly began at an earlier date than in the case of the other two forms. We know that in southern Indiana and southwestern Ohio an early retreat of the southern border of the ice took place, as is indicated by the presence of Illinoisan drift south of the early Wisconsin border (cf. Leverett, 1902, Pl. 2 and Pl. 11). There also was considerable recession of the ice of the Maumee-Miami glacial lobe in the earlier and later Wisconsin stage, while in central and eastern Ohio and western Pennsylvania (Scioto glacial lobe and Grant River glacial lobe) only in the later Wisconsin stage did recession take place (cf. Leverett, ibid., and Pl. 13 and Pl. 15). Toward the end of the later Wisconsin stage large lakes began to form in front of the receding ice, and this happened first in the western part of this region. The first lake thus formed was Lake Maumee (Leverett, p. 710 ff., Pl. 20 and 21), which had an outlet toward the west and southwest (Fort Wayne outlet; sec also Grabau, 1901, p. 58). Lake Maumee was situated in northwestern Ohio, in the present Huron-Erie basin, and thus we see that the latter was opened first in its western part to an immigration from the southwest

⁵¹ A loss of territory must have occurred in the south, *C. propinquus* losing ground in competition with *C. rusticus* which was pushing on from the south. This matter does not belong to our present investigation, but attention should be called to it.

(Indiana) at a time when this basin was entirely covered by ice further east, thus being closed more or less to an immigration from the central parts of Ohio (drainage of middle Ohio), and being closed entirely to an immigration from eastern Ohio and western Pennsylvania (drainage of upper Ohio).

This explains why *C. propinquus*, which survived in southern Indiana, had the first chance to spread northward and to enter the future Huron-Eric basin by way of Lake Maumee. The subsequent stages of this lake (Lake Whittlesey, Lake Warren, etc.), are all direct continuations in time of Lake Maumee, and so it is not astonishing that *C. propinquus*, after the final establishment of the St. Lawrence drainage,⁵² is found all over this region, not only in the Lake Huron and Lake Erie basins, but also farther down, in Lake Ontario and the Lower St. Lawrence drainage. In the occupation of this whole region *C. propinquus* was not interfered with by the other forms, since no opportunity was given to *C. propinquus sanborni* and *C. obscurus*, to enter the Erie basin, the drainages of the middle and upper Ohio remaining permanently changed to the southwest, away from Lake Maumee, a condition which obtains, with very slight changes, up to the present time.

However, C. propinquus sanborni as well as C. obscurus, have entered the Lake Eric drainage. With regard to the first, it may be sufficient to state that it is found in Lorain County, Ohio, in rivers and creeks running into the lake, and this is apparently due to a comparatively recent immigration under similar conditions as in the case of C. obscurus in Pennsylvania. The latter species has been discovered by the writer in Crawford and Erie Counties, Pa., in streams flowing to Lake Erie, associated with the Lake Eric form, C. propinquus. Thus C. obscurus must have crossed the divide between the upper Beaver (Shenango) River and Alleghany River (French Creek) on the one side, and Lake Erie (Conneaut and Elk Creeks) on the other, and the question is by what means this was accomplished.

It is only natural that *C. obscurus*, surviving during Glacial times in southwestern Pennsylvania and West Virginia, migrated up the drainage of the upper Ohio, chiefly the Beaver and Alleghany Rivers, in Postglacial times, for after the end of the Glacial Period this system formed a unit ⁵³, and no serious barriers to the dispersal were, or are, present. Thus it was easy for this species to go up

⁵² The change of the westward drainage to an eastward took place toward the end of the Glacial Period, as soon as the ice receded far enough to uncover Lake Ontario (Lake Iroquois), thus permitting the water to drain off through the Mohawk, and later through the St. Lawrence. This was accompanied probably by a depression of the land in the Northeast, culminating in the marine invasion of the St Lawrence valley (Champlain submergence). (See Grabau, 1901, p. 59 et seq.)

⁵³ As to the formation of the present Alleghany out of the former Lower, Middle, and Upper Alleghany, see Leverett, 1902, p. 129 et seq.

toward the head-waters of these rivers and to closely approach the divide toward Lake Erie.⁵⁴

This would favor a direct crossing of the divide by actual migration over land, and indeed the river-species are able to survive when out of the water for a considerable time under certain circumstances, as I have ascertained by experiments. During hot and dry weather it is hardly possible to keep them alive for more than an hour or two; but in cool, cloudy, and damp weather I have found that specimens suspended on a string on an open veranda⁵⁵ were not dead after seven hours, and restored to water, recovered entirely. This might at least render a migration over land possible, but I do not think that it actually takes place, since it has never been observed, either by others or by myself, that C. obscurus, or any other species classed ecologically with the river-species, leaves the water voluntarily. On the other hand it is possible that C. obscurus may undergo a passive transport from one drainage to the other, as for instance by birds. However, I do not believe that the crossing of the divide toward Lake Erie is due to the latter cause. It seems to me highly improbable, not that birds should be able to carry crawfishes for a long distance, but that it should happen that a bird should take up a crawfish in one stream, carrying it to another safe and sound, and drop it there without hurting it. Birds do take crawfishes 56 and sometimes carry them short distances, but this always results in serious injury, even if the specimen is not immediately eaten. Thus, even though we may admit that crawfishes might be transported by birds without being injured, such cases must necessarily be extremely rare, and do not happen often enough to effect the establishment of a species in a drainage system from which it was originally absent.

There are other considerations which make the assumption of passive transfer improbable in our case. Toward the east *C. obscurus* is (with exceptions to be discussed below) rigidly restricted to the Ohio drainage, and nowhere crosses into that

⁵⁴ At Linesville, Crawford County, I found this species in the very headwaters, almost in the springs running into Shenango River just south of Summit, which is on the divide.

⁵⁵ Particulars of one of the experiments (I have made a series) are as follows: November 9, 1905. Cloudy day. Mean temperature: 34° F. Light breeze from West-South-West, and light snow in afternoon. Specimens of *C. obscurus* suspended on strings on veranda with sonthern exposure. Beginning of experiment 9 a. m. One specimen taken in at 2 p. m., another taken in at 4 p. m., and put into water. Both alive and vigorous next morning, and were kept alive till December 18, when they were thrown into alcohol.

In midsummer, on hot days, I often observed that the vitality of *C. obscurus* becomes very low after they are only a short time out of water. They may die within an hour, without having been subject to any other injury than that caused by the removal from the water.

⁵⁶ Mr. W. E. C. Todd informs me that remnants of crawfish are quite usual in the nest of the kingfisher. I have seen, in the collection of the Department of Agriculture, Harrisburg, a specimen of *C. bartoni*, taken from the stomach of a kingfisher.

of the Susquehanna. If transport were at all probable we should expect to find that it had taken place here, as well as in the region of Lake Erie.

Further, and this is the most important objection to the transport theory, while *C. obscurus* has invaded the Lake drainage, not only in Pennsylvania, but also in New York (Genessee River), in no case has the opposite taken place namely, that *C. propinquus* has invaded the Ohio drainage. If the crossing of the divide were due to passive transport, the same cause should have acted in both directions; but *C. propinquus* is entirely absent from the Ohio system.

The latter objection holds good also with reference to another assumption, that *C. obscurus* may have crossed into the lake drainage by the aid of the old canal which connected the Beaver River with Lake Erie (Erie extension of Beaver canal). This canal (see Jenkins, 1903, p. 288, 289) was in part used as early as 1834, and was completed in 1844; it was abandoned in 1871, and it cannot be denied that by it *C. obscurus* might have been able to reach the Erie drainage. I would not hesitate to accept this as correct if it were not for the fact that *C. propinquus* has not gone in the opposite direction.^{56a} Precisely in the region of this old canal my collections are very complete, and are supplemented by those of others (Messrs. O. E. Jennings, D. C. Hughes, and W. R. McConnell), so that I am positive about the absence of *C. propinquus*.

On the other hand, we have seen that the specimens of *C. obscurus* from the tributaries of the lake seem to approach more closely those of Beaver River than those of French Creek. This would be in favor of the canal-theory, the canal running from Newcastle by the way of Shenango River to Conneaut Creek (Jenkins, *l. c.*), while French Creek was not so closely connected with it (although there was a "French Creek feeder"). The absence of *C. propinquus* in the Beaver drainage may be due to the fact that in Erie County, the canal was not so closely connected with the streams running to the lake, and that thus the lake species could not get into the canal; or else *C. propinquus* being the weaker species of the two could not make any headway against the more vigorous *C. obscurus*.

There remains another theory, namely, that the migration of *C. obscurus* into Conneaut and Elk Creeks is due to stream-piracy. The latter has undoubtedly taken place in this region in Postglacial times. The Postglacial divide between Lake Erie and the Ohio was formed originally by moraines of the late Wisconsin stage (Lake escarpment morainic system. See Leverett, 1902, Pl. 18; also Carll, 1880, Pl. 1) or by higher elevated parts of the non-morainic drift lying immediately

 5^{56a} It should, however, be horne in mind that the discharge of the water from the canal was downward toward the lake and thus that migration might in that direction have heen easier than in the opposite. — EDITOR.

in front of this morainic system. The fall of the creeks running northward to Lake Erie from this divide is much more considerable than that of those running southward, and thus it is clear that crossion on the northern slope must have been more efficient than on the other side. The consequence is that the tributaries of Lake Erie, at least some of them, have worked back through the original divide, and have captured parts of the original Postglacial drainage of the Ohio. This is most evident (see Pl. XLIII) in the cases of Conneaut and Elk Creeks, and it is just in these creeks that I found *C. obscurus* associated with *C. propinquus*,⁵⁷ while in Walnut Creek, which has apparently not entirely cut through the original divide, *C. obscurus* is not found.

Thus it is possible that the presence of *C. obscurus* in the Lake Erie drainage is due to stream-piracy. Both species, *C. obscurus* and *propinquus*, are associated here, but it seems that they are antagonistic to each other to a certain degree. In the tributaries of Conneaut Creek I found *C. propinquus* exclusively, while Conneaut Creek itself contained both, but *C. obscurus* prevailed, and it appears as if the latter had driven out the other species, which took refuge in the smaller tributaries.

We might expect to obtain some light upon the question, whether C. obscurus reached the Lake Erie drainage in consequence of stream-piracy or by the help of the canal, by the analogy offered in the Genessee drainage, but conditions seem to have been not entirely identical here. The type locality of C. obscurus (see Pl. XLII, Fig. 3) is the Genessee River at Rochester, Monroe County, New York, where this species also is found associated with C. propinquus. Mr. W. P. McConnell has discovered C. obscurus in the upper Genessee drainage near Ulysses, Potter County, Pennsylvania. The material consists of numerous males of the first and second form and of females, and there is not the slightest question that this is the true C. obscurus, no trace of C. propinquus being present here. How did this species get from the Alleghany drainage into that of the Genessee?

The drainage of the Genessce River lying entirely within the glaciated area, this must have happened in Postglacial times. Fairchild (1896, p. 423) has shown that during the recession of the ice the Genessee basin was occupied by a lake, which had its outlets in different directions successively, draining either to the Susquehanna or to the Ohio. He distinguishes ten stages, and the sixth was the last in which the water flowed to the Susquehanna; in the seventh and eighth stages Genessee Lake became connected with Lake Warren, which drained to the west into the Mississippi basin (but not into the upper Ohio), and finally the St. Lawrence drainage was

⁵⁷ The sonrces of Elk Creek are in a tamarack-swamp, which also drains to the south, to French Creek, so that some kind of a direct connection may be present. I have not visited this swamp.

established. Thus we see that in the beginning Genessee Lake was connected repeatedly with the upper Ohio (Alleghany River) drainage, but it is not probable that *C. obscurus* immigrated at this time, for then it ought also to have reached the Susquehanna drainage, since the lake discharged its water into the Susquehanna (through the "Burns outlet") subsequently to the last connection ("Cuba outlet") with the Alleghany River. (See Fairehild, 1896, map. Pl. 19.)

After this a discharge toward the upper Ohio was never re-established. But we know that stream-piracy has taken place in this region (headwaters of the Genessee), and although in some eases the Alleghany River seems to have captured parts of the Genessee drainage (Oil Creek has captured the head of Black Creek; see Leverett, 1902, p. 207), the opposite has positively also taken place, for instance, Knight Creek and Van Campen Creek have captured, according to Fairehild, small lakes that once discharged towards Oswayo Creek, a tributary of the Alleghany. This may have happened after the sixth stage of Lake Genessee, when there was no longer any connection with the Susquehanna system, and would explain the presence of *C. obscurus* in the Genessee River and its absence in the Susquehanna.

The eastern boundary of C. obscurus in Pennsylvania is formed, generally speaking, by the divide between the Ohio drainage in the west and that of the Susquehanna and the Potomae in the east. This is most evident in the northern part of this line, in Potter, McKean, Elk, Clearfield, Jefferson, and Indiana Counties. This species goes up the Alleghany River probably into Potter County, for it has been found not far away from the eounty line at Larabee, MeKean County. It has not been found in the drainage of Clarion River in Elk and Jefferson Counties, but this is very likely due to the excessive pollution of this river. There is hardly a watercourse known to me in Pennsylvania which is in a worse condition than Clarion River in Elk County. The wood-pulp mills at Johnsonburg, the tanneries at Ridgway, the chemical factory at St. Mary's discharge refuse into it, and Toby Creek adds sulphur water from the mines above Broekwayville (Jefferson County). Similar conditions prevail in Red Bank and Sandy Lick Creeks in Jefferson County, but I have been able to ascertain the presence of this species near the head of Sandy Liek Creek at Dubois, Clearfield County (about 10 miles from the divide).⁵⁸ In southern Jefferson County, C. obscurus is not present in Mahoning Creek at Punxsutawney (although C. bartoni was there), this creek being slightly polluted by minewaters; but I found it here in a pond connected with the creek. In Indiana County it is present in all creeks running to the Alleghany and Conemaugh (Little

⁵⁸ I found this species here on June 16, 1905. Only two living specimens were taken, hut numerous dead ones were lying in the creek. Apparently some injurious substance had been quite recently introduced into the water.

Mahoning Creek, Crooked Creek, Two Lick, and Yellow Creeks). Crossing over the divide in this region into the drainage of the West Branch of the Susquehanna, no trace of this species is found. I hunted for it in vain in Sinnamahoning Creek in Cameron County, in the West Branch and its tributaries in Clearfield, Cambria, and Indiana County (near Cherry Tree), and in Clearfield Creek in Cambria County.

In this whole region (headwaters of the West Branch) stream-piracy has takenplace on a large scale, the whole basin of this river having been taken away from the original Alleghany drainage. But *C. obscurus* has not been taken over. According to Davis (1889, p. 248, see also above, p. 430) this stream-piracy fell largely into Pretertiary times, and although we are to assume that it continued during subsequent times (p. 430), it must have been rather slow, and insignificant, chiefly so in Glacial and Postglacial times, which alone are to be considered in the case of *C. obscurus*. Although this species was present in the Alleghany River drainage, it did not go up into the headwaters, remaining away from the actual divide for a distance of about ten to twenty miles. Under these circumstances, as stream-piracy was only going on at the headwaters, no good opportunity was offered for this species to cross the divide.

In Cambria County the continental divide bends to the east, and is transferred to the main chain of the Alleghanies (Alleghany Front); but the eastern boundary of *C. obscurus* does not follow it. Here it is the Chestnut Ridge which constitutes the boundary, beginning in southern Indiana County, and continuing through Westmoreland and Fayette Counties to the southern state-line. Generally *C. obscurus* does not pass beyond this ridge into the higher parts of the Alleghany Plateau, but there are two exceptions. It is found in the Loyalhanna River in the Ligonier valley, and in Indian Creek, and in this region it is not the Chestnut Ridge, but the Laurel Hill Ridge which forms the eastern boundary. In the Conemaugh River and the Youghiogheny, this species has not been able to pass upstream beyond the Chestnut Ridge, since both rivers become very rough above this point, and this roughness apparently existed also at the end of the Tertiary Period, when the rivers descended, through the Chestnut Ridge, from the elevated Old Tertiary peneplain to the late Tertiary base-level, at which they were then flowing.⁵⁹

⁵⁹ According to Campbell (1903, p. 292) the peneplain of southwestern Penusylvania, elevation 1200 to 1300 feet, is identical with the Old Tertiary Harrisburg peneplain; and according to White (1896, p. 377), the Old Monongahela (with the Youghiogheuy) of Late Tertiary age was about at hase-level. Stevenson (1878, p. 259) has called attention to an old terrace of the Youghiogheuy at Councellsville, which apparently corresponds to the late Tertiary hase-level, 200 feet above the present level (894 feet) at about 1100 feet ahove the sea. At Coufluence it is 1820 feet high, thus giving to the river between Coufluence and Connellsville a fall of ahout 700 feet at the end of the Tertiary. At present the fall of the river is only 432 feet between the points named. Although the identity of the old terraces is not demoustrated, the difference of elevation is so great that a considerable fall of the Tertiary river is beyond doubt, and thus at that time a barrier to the upstream dispersal of *C. obscurus* must have existed here.

As has been repeatedly mentioned, *C. obscurus* has been discovered in Wills Creek, a stream which belongs to the Potomac drainage, at Hyndman, Bedford County, Pennsylvania, and Ellerslie, Maryland. This locality is entirely isolated and about 40 to 50 miles distant from the nearest parts of the main range in Westmoreland and Fayette Counties, separated from the latter by that part of the Alleghany Plateau which is included between Chestnut Ridge, Laurel Hill Ridge, and the Alleghany Front. In this region, chiefly in the drainage of the upper Youghiogheny and Castleman Rivers, *C. obscurus* is missing, of which fact I am quite positive, having searched for it in vain at the following localities : the Youghiogheny River at Ohiopyle, Fayette County, same river and Laurel Hill Run, Confluence, Somerset County ; Youghiogheny River, Selbysport, Garrett County, Maryland ; Castleman River, Rockwood, Somerset County ; Flaugherty Creek, between Meyersdale and Keystone, Somerset County.

Under such conditions stream-piracy is out of the question. For some time I suspected that *C. obscurus* might be present in other parts of the upper Potomac drainage, but this is not the case. I have investigated the Potomac River at Cumberland, Maryland, and above Cumberland (Rawlings, Alleghany County, Maryland), and further up, where it forms the boundary between Garrett County, Maryland, and Mineral and Grant Counties, West Virginia; but I have not seen a trace of this or any other river-species. Below Cumberland *C. limosus* turns up. Thus the presence of *C. obscurus* in Wills Creek is very local, and restricted to only a small part of the creek. I found it at Ellerslie, Maryland, but not below this point, although I investigated the whole creek from Mt. Savage Junction to the Pennsylvania state-line. At Hyndman it is quite abundant, but only below a point about half-a-mile south of the railroad station, thus occupying only about eight or nine miles of the creek.

These facts are rather strange, and, I believe, can only be explained by the assumption of artificial introduction by human agency. I do not think that it was necessarily intentional, but it may be due to accidental stocking of the creek with this species, which is not altogether improbable, if we consider that in this region a good deal of fishing is done, and that fishermen from places between Pittsburgh and Connellsville go over this whole region, and frequently use crawfishes as bait, capturing them in one part of the country, and carrying them for their purposes to other parts. If *C. obscurus* has not been transported in this way to Wills Creek, intentionally or accidentally, I have no other explanation to offer.

The above theory as to the origin of the distribution of the group of *C. propinquus* explains the facts, as far as I can see. Our knowledge of the distribution of

C. propinguus and of C. propinguus sanborni is rather unsatisfactory, but none of the known faets is opposed to our theory. With reference to C. obseurus in Pennsylvania, I think our assumptions are well supported. Cambarus obscurus is a Preglaeial form, belonging to the Old Monongahela (or Spencer) River, which survived during Glaeial times in the headwaters of this river (Lake Monongahela), and spread out, in Postglaeial times, over the whole of the Upper Ohio drainage (in addition to the Ohio and Monongahela, over the drainages of the Beaver and the Alleghany Rivers), and was only elecked in its dispersal in the direction toward the mountains by the roughness of the streams. The Ohio River of Postglaeial times opened a way down stream, but C. obseurus was unable to spread in this direction, since these parts were occupied by another elosely allied species, C. propinguus sanborni. It has slightly entered upon the territory of the latter (Fishing Creek), but has not been able to erowd it out or to eonquer it. Similar conditions prevail in the Lake Erie drainage, which has been reached in consequence of stream-piracy, or else, by the help of modern eanals. Here it eame into contact with C. propinguus. In both eases (in West Virginia and Erie County, Pennsylvania) we see that the other species show indications of an inclination toward C. obscurus. I believe we have to deal here with hybridization, but this will be discussed later. Finally the species has crossed over into the Lake Ontario drainage in the region of the headwaters of Genessee River, presumably in eonsequence of stream-piracy. In the upper part of this system, in Pennsylvania, it did not find any competition, and is alone represented there, while in the lower part, at Rochester, N. Y., it is again found associated with C. propinquus. Further details with respect to these parts are not at hand.

Comparing the distribution of the *propinquus*-group with Adams' scheme of Postglaeial dispersal of the biota of North America, we see at a glance that the whole group belongs to his *northeastern biota* of the *second wave* (Adams, 1905, p. 58). The biotic preserve of this element, during glaeial times, was not far from the southern edge of the iee, in what is now the Ohio drainage, but it was restricted to this western part, and was not extended east of the Alleghany Mountains. In Postglaeial times this group advanced northward, forming part of the second wave, which is most elearly seen in the present distribution of *C. propinquus*, which largely entered the coniferous forest-belt in Miehigan, New York, and Canada. The other two forms (*C. propinquus sanborni* and *C. obseurus*) did not take much part in the migration of this wave, since they found a barrier to the north in the shape of the eontinental divide, and then, after they had erossed this divide at eertain points, they found competition in *C. propinquus*, which had populated the whole St. Lawrenee drainage at an earlier date ("bioeenotie barrier"). In New York state,

however, *C. obscurus* has advanced north in the Genessee basin to a considerable distance.

3. Cambarus bartoni.

a. Summary of Facts. (Sec pp. 381–386.)

Cambarus bartoni is very uniformly distributed all over the state, being, however, rather scarce in the extreme northwest in Erie County, where it is replaced by the form *C. bartoni robustus*. We shall discuss this later.

The species extends considerably beyond the limits of this state, chiefly toward the southwest and northeast. In these directions it ranges from Tennessee and North Carolina to New Brunswick and Quebec. Westward it reaches central Kentucky and southern Indiana. The Atlantic Coastal Plain is apparently not invaded by it to any considerable degree.

We clearly see that its range follows the main strike of the Appalachian system, and knowing that coologically this species is a form of the rapid and cool waters of the uplands and mountains, living preferably in small streams and even springs, we understand that the distribution must be entirely different from what we have learned with reference to the river-species already discussed.

In Pennsylvania conditions seem to be favorable for this species everywhere, possibly with the exception of a very narrow strip on the eastern border, along the Delaware River (coastal plain); but even here it approaches the lowlands very closely, the Piedmont Plateau reaching the river at many places.

In the mountains elevation is no barrier for it, I found it myself at 2,600 feet on Laurel Hill Ridge, west of Jennerstown, and at 2,300 feet near Sandpatch, Somerset County, and at other places at elevations not much less (Chestnut Ridge in Westmoreland County; near Cresson, Cambria County; Keating Summit, Potter County). At Davis, Tucker County, West Virginia, I collected it in Blackwater River at 3,050 feet, and Faxon, 1898, p. 649, records it from Roan Mountain, North Carolina, 6,000 feet.

b. Origin of the distribution of C. bartoni.

The first point is to ascertain the center of radiation of this species. As I have pointed out in a previous paper (1905, p. 121), we must regard the southern section of the Appalachian system as the original home of the subgenus *Bartonius*, to which this species belongs, and (*l. c.*, p. 122) the advance and dispersal of the subgenus took place over the castern mountains of the United States, the axis of the dispersal being directed from southwest to northeast.

We have reason to believe that the origin of this species falls into Preglacial times, it being rather primitive within the subgenus (at least in comparison with the

diogenes-group). If this is the case it very likely extended in the Tertiary at least as far north as at present, but the advancing ice of the Głacial Period must have driven it south again, and it must have survived in the mountains of Virginia, West Virginia, and states further south. Possibly southern Pennsylvania formed part of its preserve in Glacial times, for the peculiar preference of this species for cold water admits this assumption. Be this as it may, it is certain that after the retreat of the ice this species advanced, occupying or reoccupying the whole state of Pennsylvania, and keeping on in its northward migration, until finally reaching its present range.

This advance in a northeastern direction clearly agrees with Adams' third highway of dispersal (1902, p. 123) along the Appalachian chain, and C. bartoni also belongs to the northeastern biota of the second Postglacial wave (1905, p. 58). What is interesting in this case is that an aquatic creature follows here the main strike of the mountains, independent of the drainage systems. I have previously called attention to this fact (1905b, p. 129), and have pointed out that this is rather the rule with the subgenus Bartonius (this has been observed already by Faxon, 1885a, p. 179). There is not the slightest doubt that this peculiarity is connected with the ecological laws governing this species. It lives generally in the region of the headwaters of the streams, where the dendritic conformation of the drainage systems and their mutual interlocking favors frequent shifting of the divides in consequence of stream-piracy.

Moreover, *C. bartoni* is a form which habitnally leaves the water. It is found not only in small streams, but also in springs, often at places where there is a very scanty supply of water, and this has forced it to often assume burrowing habits. Like *C. obscurus* it is able to survive exposure to the open air for a considerable time, provided the temperature is not too high, and thus it is easy to imagine that it may cross over divides during rainy or cloudy weather, wandering from spring to spring in the mountains. On the other hand, we see that *C. bartoni* is not entirely absent from larger streams, and if once established in a small part of the drainage of a certain river it may easily be distributed over the rest of it by simply following the course of the stream. Thus it is not strange that this species has occupied the whole of the state, and this uniformity of distribution is chiefly due to the fact that the whole of Pennsylvania is hilly or mountainous, offering everywhere favorable conditions for this species. The general dispersal is due to two causes : first the ability of this species to cross watersheds by active migration ; and second to stream-piracy, which has apparently played a considerable part in its dispersal.

It should be noted, as we have seen above, that the size of this species decreases

markedly in the eastern section of the state. This fact is significant, in so far as it points out that the center of radiation for the state of Pennsylvania is rather on the western side of the mountains than on the eastern (see Adams, 1902, p. 122, "fourth criterion for the determination of centers of dispersal").

4. Cambarus bartoni robustus.

a. Summary of Facts. (See pp. 390-391.)

This form is found in Pennsylvania in a rather continuous area in the extreme northwest, in McKean, Warren, Erie, and Crawford Counties, both in the Alleghany River and the Lake Erie drainages. It is often associated with the typical *C. bartoni*, but has been found at different localities in Erie County without the latter. In addition it is not rare in the northeastern part of Allegheny County in the Alleghany River, and its tributaries, and has also been found in Chartiers Creek, in southwestern Allegheny County. Here it is always associated with the typical form.

In no other part of the state has this variety been discovered, and it is very important to note that no trace of it has been found in southwestern, central, southern, and eastern Pennsylvania. Although *C. bartoni* is abundant in these parts, and particular attention has been paid to the possible presence of *C. bartoni robustus*, all attempts to find it have failed, and I feel justified in asserting that it is absent here.

I am not so sure of this with reference to the region between Crawford and Warren Counties on the one side, and Allegheny County on the other. I have searched in this section for *C. bartoni robustus*, for instance near Tionesta, Forest County, at Oil City, Venango County, in Mercer and northern and central Butler Counties, and near Kittanning and Mosgrove, Armstrong County, but did not discover it. However, it is possible that it is present along the course of the Alleghany River, in the river itself, and some of its tributaries, in Forest, Venango, and Armstrong Counties. In some of the places mentioned I did not strike streams which looked very favorable, being generally not large enough. Yet in Erie and Crawford Counties I sometimes found this species in rather small streams. Conditions in Otter Creek, Mercer County, Slippery Rock Creek and Thorn Creek, Butler County, were apparently identical with those under which it is generally found in Erie County, but this form was not found.

b. Origin of the distribution of C. bartoni robustus.

Considering that the true *C. bartoni robustus* is a northern form, being found outside of Pennsylvania in northern Ohio, western New York, and Canada (St. Lawrence Basin), its center of distribution seems to be at the northwestern edge of the range of *C. bartoni*, in the St. Lawrence drainage. In Pennsylvania, however,

it has crossed the continental divide, and has invaded the Alleghany River drainage in McKean, Warren, and Crawford Counties, and possibly has come down the Alleghany River as far as Allegheny County, spreading into some of its smaller tributaries.⁶⁰ This assumption seems plausible if we take into consideration only the Pennsylvanian material and that from the St. Lawrence Basin. We would have here a case of distribution which is entirely unique. *C. bartoni robustus* should then be regarded as a Postglacial form, which originated in the St. Lawrence drainage, and in Pennsylvania spread southward, coming from the north.

But there are objections to this view. *C. bartoni robustus* has been reported also from Virginia, Maryland, and Kentucky, and this, of course, would not be in favor of this theory. However, as has been said above (p. 392), I am inclined to believe that this southern form is not the same as the northern. If this view should be correct, I should regard *C. robustus* as a good species, and then the above opinion would hold good.

But further, the morphological characters of *C. bartoni robustus*, as compared with those of the typical *bartoni*, are distinctly more primitive. The shape of the rostrum is decidedly more archaic, the original form of the rostrum in the subgenus *Bartonius* being rather elongate, and not short and broad as in *C. bartoni*. The frequent presence of distinct lateral spines on the carapace is undoubtedly a primitive character; and the ecological peculiarity of preferring larger streams than are haunted by the typical form might also be regarded as a remnant of more primitive conditions. This, of course, would be strange in a Postglacial form, originating within the glaciated area, and we rather ought to expect a higher differentiation than the original, typical form.

Until the question of the identity of our northern *C. bartoni robustus* with the southern form, which bears the same name, is settled, we cannot form a final opinion. If both forms should be actually identical, we might have to deal with two races of *C. bartoni*, an older one (*C. bartoni robustus*), which possibly constituted a first wave of migration from southwest to northeast, which was overrun and crowded out by a later wave, consisting of *C. bartoni typicus*. Remnants of the older stock have been able to survive only at a few, scattered localities in the south, while in the

⁶⁰ The Alleghany River, between Sandy Creek and Verona, bas been investigated repeatedly. It is a curious fact that Dr. D. A. Atkinson collected here a large number of *C. obscurus* on September 17, 1900, but not a single *robustus*. I was at the same place on June 1, 1904, together with Dr. Atkinson and Dr. O. T. Cruikshank, but we did not collect this form (conditions were unfavorable); on November 19, 1904, I spent a whole day there, collecting numerous *C. obscurus*, and a few *C. bartoni* (typical), but not a single *robustus* was seen. When 1 visited this place again, on September 7, 1905, I seenred within a short time six specimens of *C. bartoni robustus*, and on September 30, 1905, I found three fine specimens a little further up the river, at Hulton, although I did not hunt very diligently. Is it possible that the migration of this form down the river is going on? Does it gradually become more abundant?
northwest a more continuous and solid colony has remained. The scarcity or even absence of the typical *bartoni* in Erie County, Pa., which in our state is the chief domain of *C. bartoni robustus*, would support this view. *C. bartoni* has not yet invaded this region to such a degree as to crowd out the other form. Though I must confess that it does not strike me as very likely that the smaller form should be able to conquer the larger one.

Further investigations on this question should be made outside of this state.

5. Cambarus carolinus.

a. Summary of Facts. (See pp. 396-397.)

This species (see Pl. XLIII) is found in Pennsylvania in the southern part of the Alleghany Plateau, between the Chestnut Ridge in the west, and the Alleghany Front in the east, preferring the high valleys in this region, but not going up to the highest elevations of the mountains. Thus, although abundant near Meyersdale in Somerset County, it does not go up the valley of Flaugherty Creek toward Sandpatch. I have searched for it in vain between Meyersdalc and Keystone, and at Sandpatch. In a northern direction this species ranges in the valley between the Chestnut Ridge and the Laurel Hill Ridge as far as southern Westmoreland County. Here the northern boundary is formed by the cross-divide in this valley separating the headwaters of Indian Creek from the Ligonier Valley. I am quite positive of this boundary, since I have searched in vain for chimney-builders all over Ligonier Valley from Idlepark (below Ligonier) to the sources of the Loyalhanna River. Coming across the divide to Jones' Mills, within a short time I discovered this species. In the longitudinal valley between the Laurel Hill Ridge and the Alleghany Front, this species has advanced further north. It has crossed the divide between the Castleman River drainage and that of Stony Creek (tributary to the Conemaugh), and I found it near Listie and Windber, in Somerset County. At the latter place it seems to attain its northern boundary. At all events I failed to find it near Lovett in Cambria County, in the high valley of Laurel Run, which to all appearance affords congenial conditions for its presence being rather swampy in many places. I have also searched for it unsuccessfully in the region of Cresson, Cambria County, and at several places further north.

The rest of the range of this species is entirely to the south of this state, in Maryland, West Virginia, Virginia, North and South Carolina (disregarding the isolated report from the Indian Territory, in which I do not put much faith). No particulars are known about its boundaries, but in this region also it is restricted to the mountains.

b. Origin of the distribution of C. carolinus.

Generally, conforming to the subgenus *Bartonius*, the center of radiation of this species is to be sought in the southern part of the Appalachian system. It has followed in its migration the strike of the mountains, keeping to the higher parts of the latter. Thus it has entered southern Pennsylvania, being restricted here to the highest portions of the Allegheny Plateau.

The lowest elevation at which I found it is at Ohiopyle, Fayette County, 1,250 feet, and at Dunbar, Fayette County, 1,260 feet. (At the latter place a few stragglers — two specimens — were taken as low as 1,070 feet, associated with *C. diogenes*, but here they had apparently come down from the top of the mountain, where this species was abundant at 1,260 feet.) All other localities in Pennsylvania were higher, generally between 1,500 and 2,000 feet.

The northern boundary of this species in our state is formed by two different, opposite features in the physical geography. Between Chestnut and Laurel Hill Ridges it is a cross divide of the longitudinal valley; between Laurel Hill and the Alleghany Front the deep erosion of the original longitudinal valley by the head-waters of the Conemaugh River forms the boundary. We do not know much of the geological history of this region, but it seems to me that the floors of these high valleys with their extensive clay deposits form a part of a former base-level, namely, that of the Old Tertiary peneplain identified with the Harrisburg peneplain by Campbell (1903, p. 293). In northern Somerset and southern Cambria Counties this has been eroded by the Conemaugh system, thus removing a good deal of the clay bottoms, which seem to be an essential condition for this species, and consequently the lack of this feature, or its interruption by the Conemaugh system at the northern end of Somerset County, has formed here the barrier to the dispersal of *C. carolinus*.

To all appearances *C. carolinus* is a Postglacial immigrant into this state. The northern boundaries in both of the longitudinal valleys are rather insignificant, and we should expect that *C. carolinus*, being a chimney-builder and able to leave the water for a considerable time, should be able, like *C. bartoni*, to cross boundaries of this character. We should even expect that it would be better fitted to do so than *C. bartoni*. In fact *C. carolinus* must have done so repeatedly on its way from the South, being found in the upper drainages of rivers running in different directions, for instance, the upper Youghiogheny in Maryland, the upper Potomac in Maryland and West Virginia, upper Decker's Creek (tributary of the Monongahela), and upper Cheat River in West Virginia.⁶¹ That it has been checked in Pennsylvania

⁶¹ As to stream adjustments and migration of divides in Garrett County, Maryland, See Abbe, 1902, p. 47, 53.

by such minor barriers as an insignificant divide and a deeply eroded system of valleys, renders it very probable that these obstructions are only temporary, and may be overcome in time, and, on the other hand, that the immigration of this species is rather recent, its northward migration being not yet finished, but only temporarily stopped.

The fact that this species is restricted to a narrow strip within the mountains is clearly due to its ecological habits. It prefers a certain altitude and clay bottoms. The latter are found in Pennsylvania chiefly on the Old Tertiary base-level, and this is represented to a large degree only within the mountains. East of the Alleghany Front and west of the Chestnut Ridge only insignificant remnants of this base-level are found, and thus this species is missing.

We do not know anything about the Preglacial history of this species, and the facts at hand furnish no evidence with regard to this question. According to the morphological characters, and compared with *C. diogenes* and *C. monongalensis*, we must assume Preglacial age for it. Its immigration into Pennsylvania probably is Postglacial, and thus it possibly belongs to Adams' *third wave* of migration, starting from the *southeastern* center (Adams, 1905, p. 62). However, in analogy to *C. monongalensis* it may belong to the *second wave*, and the *northeastern biota* (see below under *C. monongalensis*).

6. Cambarus monongalensis.

a. Summary of Facts. (See pp. 400-401.)

Cambarus monongalensis occupies in Pennsylvania (see Pl. XLIII) a continuous area in the southwestern part of the state. Toward the east, beginning at the southern state-line, the limit of the distribution is formed by the Chestnut Ridge as far as the point where the Loyalhanna River cuts through this ridge in Westmoreland County. From this point the boundary follows the Loyalhanna to the north, and continues northwestward along the Kiskiminetas River. From the point where the Kiskiminetas empties into the Alleghany, the latter river, and further down the Ohio, form the northern boundary of this species, until the Ohio leaves the state in Beaver County.

Within this area this species has been found wherever it has been searched for, namely: in Greene, Washington, and southern Beaver Counties; in the northwestern section of Fayette County; in the larger part of Westmoreland County, and in southern Allegheny County. It has also been traced beyond the boundaries of the state in a western and southern direction: it is found all over the Panhandle of West Virginia (Hancock, Brooke, Ohio, and Marshall Counties), and has also been

found at Morgantown, Monongalia County. It undoubtedly goes further south in West Virginia, but no records are at hand from these parts.

The writer was unable to discover this species in the state of Ohio (Harrison, Carroll, and Stark Counties), and its absence north of the Ohio-Alleghany River is well established (with one exception to be presently mentioned). Particular pains have been taken to ascertain the latter fact. While it is very abundant in Allegheny County, south of the Alleghany and Ohio Rivers, the writer has not in a single instance found it north of them. He has searched in vain at many localities in northern Beaver, northern Allegheny, in Armstrong, and Butler Counties, and further north. At one single locality, however, on the northern side of the Alleghany River it is present. It was found by Dr. D. A. Atkinson near Squaw Run, at Aspinwall, Allegheny County (more correctly near Claremont). This seems to be a very restricted locality. The writer did not visit it himself, but he hunted all over the region around it from Aspinwall to Squaw Run, and beyond to Montrose, Powers Run, and Harmarville, without discovering additional localities for the species. Thus it seems that this locality is the only one on the northern side of the river, and we are able, as we shall see below, to explain its presence there.

This species is generally found at elevations from 900 to 1,200 feet; and it rarely descends to 800 feet or less. The lowest altitude at which it was found is 790 to 800 feet at Colliers, Brooke County, West Virginia, and at about the same (estimated) elevation it occurs in Fern-Hollow and Nine-Mile Run, Pittsburgh.

b. Origin of the distribution of C. monongalensis.

The distribution of this species outside of the state is very incompletely known, and consequently we cannot form any opinion as to its center of dispersal. Considering, however, that it is clearly a form cognate to *C. carolinus*, we may safely assume that it also came from the south, from West Virginia. *C. carolinus* and *C. monongalensis* seem to be two parallel species, closely connected genetically, the one belonging to the Old Tertiary base-level within the mountains, (elevation 1,200 to 2,000 feet), the other to the hills west of Chestnut Ridge (elevation 900 to 1,200 feet), formed by the Tertiary erosion of this base-level. The areas of both are separated by the escarpment of the Chestnut Ridge, and both have probably migrated on parallel lines.

C. monongalensis must have invaded Pennsylvania and the Panhandle of West Virginia from the south, being confined to the region between the Chestnut Ridge and the Ohio River. That in this case a large river forms a barrier to an aquatic creature is highly interesting, but is easily explained by the ecological habits of the

species. Living underground near springs, and positively avoiding even the smaller streams, it is clear that a large river does not offer congenial conditions, and that it even may become dangerous to single individuals when they are accidentally swept into such a stream, they then being unable to get out and reach more favorable locations.

The restriction of this species to a comparatively small area in southwestern Pennsylvania is thus easily explained. The northward expansion was stopped by the first large river flowing from east to west in this region.

A few additional points need discussion. Coming from the south, this species migrated largely in the direction of the great tributary of the Ohio, the Monongahela, and this river did not offer a barrier. It is different with the Youghiogheny. The latter comes through the Chestnut Ridge, and should form a barrier to the cast, preventing it from entering Westmoreland County and eastern Allegheny County, On the other hand we see that this species has in one instance crossed the Alleghany River. I do not think that this is due to direct and actual crossing of the rivers, but to a shifting of their courses, of which we have many evidences. The geological history of the rivers of this region is as follows. The highest elevations of the country between Chestnut Ridge and the Ohio River are very uniform, rarely going beyond 1,200 or 1,300 feet. This scems to represent an old base-level, belonging to Old Tertiary times, according to Campbell (1903, p. 292 ff.). This was again cut into by a drainage system belonging to the Old Monongahela or Spencer River, which, at the end of the Tertiary, was running again at basc-level (White, 1896, p. 377), at an elevation of about 900 fect (in the region of Pittsburgh), having eroded its valley about 300 fect below the Old Tertiary base-level. This river was rather sluggish and frequently formed ox-bows. The most important old channels, having regard to the matters in hand, are in the first place those which are marked by a terrace about 225 feet above the present river (at Pittsburgh), both along the Youghiogheny and Monongahela, at McKcesport, Allcgheny County, to the cast of the present rivers, which, consequently, have been shifted to the west (Jillson, 1893, p. 12, pl. 1). East of Pittsburgh we have an old ox-bow of the Monongahela in the "Wilkinsburg Valley" at about the same level (Jillson, ibid., p. 8 ff.). Here also the river has been shifted to the west. These instances are sufficient to show that repeatedly and at various places opportunities were offered to C. monongalensis to passively cross the Youghingheny and the Monongahela Rivers on account of the shifting of the latter, and the same seems to be the case with reference to the Allegheny River in the region of Squaw Run. According to Jillson (l. c., p. 10), there is a terrace 250 feet high belonging to the same general level as those mentioned above, one to two miles

north of the Allegheny in the region of Claremont. At the same place there is another terrace north of the river, only 150 feet high, and consequently belonging to a later period, so that here the final shifting of the river to the south took place later than in the other cases.

These facts, if they at all influenced the distribution of *C. monongalensis*, and I believe they did, give us a hint as to the time of the immigration of this species. The shifting of the rivers must have taken place sometime during the Glacial Period, for we know that during this time a considerable amount of erosion was accomplished, the 900 feet level belonging to the beginning of the Glacial time (Lake Monongahela stage).⁶²

This leads us to the conclusion that *C. monongalensis* must have been present in this region during the Glacial Period, at least during a part of it, and shortly before these channels were changed.⁶³ It is quite possible that this species had its preserve in Glacial time not far from the edge of the ice in southern Pennsylvania and northern West Virginia, and that it began to advance as soon as the ice of the Wisconsin stage began to recede. This would fully explain the fact that this species was able to cross first the Youghiogheny and Monongahela by the help of the westward shifting of these rivers, thus opening a way into eastern Allegheny and Westmoreland Counties, and that it later crossed the Alleghany River at Claremont, when its channel was changed to the present more southern position.

The question remains, why *C. monongalensis*, having crossed the Alleghany, did not advance further north. It is found at Claremont (near Squaw Run), in a comparatively restricted locality, which is not altogether favorable, being at a rather low elevation. It has not been able to reach more favorable locations at higher levels, the ascent being more or less difficult on account of the very precipitous hillsides, and moreover it may not prosper here because of the presence of the competing species, *C. diogenes*, which is quite abundant in this region. *C. monongalensis* is here, so to speak, cornered, and surrounded by unfavorable physical, ecological, and biocenotic conditions.

If this species existed in this region during Glacial times its Preglacial origin

⁶² The rivers were cut down even deeper than they are at present, but the valleys were filled up again, 100 feet or more (see Jillson, l. c.). According to Foshay (1890, p. 402), the chief erosion falls into the end of the Tertiary ; but the presence of glacial material in the old river channels, 900 feet high (East Liberty, Pittsburgh), places the deepening of the valleys at a later period. Possibly it was connected with and subsequent to the draining off of Lake Monon-gahela (Wnite, 1896, p. 375). which happened sometime during the Glacial Period. Hice (1903, p. 29) places this eutting down helow the present channels between the Kansan and the Wisconsin stages.

⁵³ The same conclusion is reached when we consider that this species cannot have immigrated before the present Ohio was formed, that is to say, shortly before the Wisconsin stage (see last footnote). Otherwise the Ohio would not form its western boundary.

becomes rather probable. This is in keeping with the morphological characters, as compared with *C. diogenes*, for the latter, as we shall see below, is very likely also preglacial.

We have no evidence as to the Preglacial history of *C. monongalensis*. It may, however, be said, that it must have come from the original home of the subgenus *Bartonius* in the southern Appalachians. How far north it extended in Preglacial times we do not know, but the advancing ice cannot have driven it back very far. This is very probable because it is a form decidedly partial to cold water. With reference to its Glacial-Postglacial migration it belongs to the *northeastern biota* and the *second wave* of Adams; but its advance was apparently checked at an early date by the Ohio-Allegheny River.

It will be remembered that with reference to C. carolinus another view has been expressed (p. 453). In the case of that species we do not possess any facts which enable us to fix its time of immigration into Pennsylvania with the same probability as in the case of C. monongalensis. The present extension of the range of C.carolinus in the southern mountains classes it rather with the southeastern biota. On the other hand, we know nothing about the southern range of C. monongalensis, and thus it is at present impossible to properly compare these two species. Their close affinity, however, and the identity of the ecological conditions under which they are found (aside from the difference in altitude) render it rather probable that the parallelism observed between them in some respects may reveal itself also in others.

7. Cambarus diogenes.

a. Summary of facts. (See pp. 405-407.)

Aside from a narrow strip along the Delaware River, in Delaware, Philadelphia, and Bucks Counties in eastern Pennsylvania, this species covers a large area in southwestern Pennsylvania, namely all the region occupied by *C. monongalensis*, and, in addition, a belt of a certain width to the north of it (see Pl. XLIII). Here the eastern boundary is formed, as in the case of *C. monongalensis*, by the Chestnut Ridge, but it is continued beyond the Loyalhanna River, extending into Indiana County, and then it follows the divide between the Susquehanna and Allegheny drainages as far north as the southern extremity of Jefferson County. From this region the boundary runs in a westerly direction.

In Jefferson County I found this species at Punxsutawney, and I have seen chimneys rather abundantly to the east of this place, when riding on the Buffalo, Rochester, and Pittsburgh Railroad, about as far as Big Run, Jefferson County. But

this species is not present in the neighborhood of Du Bois and Falls Creek in Clearfield County, although favorable localities are numerous there. In the valley of Red Bank Creek I have looked for it in vain near Brookville, Jefferson County. Further west the boundary becomes obscure, and is marked by the following localities: Kittanning in Armstrong County; Renfrew and Branchton in Butler County; and Mercer in Mercer County. At all events I found this species at the places named, but not north of them. Since no apparent physical feature marks the boundary in these parts, it remains doubtful whether this is the actual northern limit of distribution; but we can narrow down the zone in which it must be situated by naming a few more northern places where I searched for it in vain at the proper places: Goodville. Indiana County;⁶⁴ Templeton, Armstrong County (swampy places of the Alleghany river-bottoms); Oil City, Venango County; the region of the Pymatuning Swamp near Linesville and Summit, Crawford County. It seems, however, that toward the west the boundary has the tendency to run in a northwesterly direction, and in Ohio this species reaches the Lake Erie drainage in Lorain County (Oberlin).

Within the region above defined this species is generally found at a slightly lower altitude than *C. monongalensis.* It is, however, not preëminently characteristic of the river-bottoms, as I formerly believed (1905*a*, p. 400), but is chiefly distributed at an elevation of about 900 feet (more or less), that is to say, at about the level of the valley of the Old Monongahela River of Preglacial times. At the foot of the Chestnut Ridge it goes up to 1,200 feet and more, the highest point being Donohoe, Westmoreland County, 1,260 feet, but on the other hand it descends to the riverbottoms, between 600 and 700 feet, the lowest elevation observed being on the Ohio river-bottoms at New Martinsville, West Virginia, about 600 feet. Thus *C. diogenes* is quite abundant at about 900 feet, where *C. monongalensis* is decidedly rare; above this *C. diogenes* is rare, while *C. monongalensis* has its chief domain at this level; and below 900 feet *C. diogenes* is also abundant, while *C. monongalensis* is found only in exceptional cases.

While the boundaries of this species in Pennsylvania are tolerably well known, it is quite different with the rest of the range. It appears that the range is divided into two unequal, discontinuous parts, an eastern and a western. The eastern comprises, aside from the small section of Pennsylvania along the Delaware River, the whole or portions of New Jersey, Delaware, Maryland, the District of Columbia, Virginia, and North Carolina. Here it seems to be found exclusively in the Coastal

⁶⁴ This is in the same valley as at Punxsutawney, but C. diogenes is positively not found here, since a splendid place was found for it where it ought to have been discovered if at all present in the neighborhood.

Plain, not even entering the Piedmont Plateau. The western range begins in southwestern Pennsylvania and northern West Virginia, and we have seen that it here belongs chiefly to the late Tertiary base-level of the rivers. But in Pennsylvania it has entered the glaciated area (Lawrence and Mercer Counties), and thence has spread westward over the states of Ohio, southern Michigan, Indiana, Illinois, Wisconsin, southern Minnesota, and Iowa. Its main range is here in the glaciated region. But it also occupies localities south of the drift, in Indiana, Kentucky, Illinois, Missouri, Kansas, Arkansas, Mississippi, and Louisiana, extending westward to Colorado.

b. Origin of the distribution of C. diogenes.

The first point to be ascertained is whether there is actual discontinuity between the eastern and western range of this species. In western Pennsylvania I have positively located an eastern boundary for this species. It is formed by the divide between the Susquehanna and the Alleghany in the north, further south by the Chestnut Ridge. In the northern parts of West Virginia I am also positive that it is not found east of the Chestnut Ridge in Preston and Tucker Counties. We have the report of Faxon (1885a, p. 71) that this species is found at Deer Park, in western Maryland, but, as we have seen, this is erroneous (p. 406, footnote 27), and the species is absent in this whole region. I have searched for it in vain in Somerset and Fayette Counties (east of the Chestnut Ridge) in Pennsylvania, in Preston, Tucker, and Mineral Counties, West Virginia, and in Garrett and Alleghany Counties, Maryland. East of the Alleghany Front, in the Alleghany Mountain region, in the Great Alleghany Valley, and the Piedmont Plateau it is positively absent. It has never been recorded from anywhere within these physiographical divisions, and I myself made special search for it in Bedford, Blair, Fulton, and Franklin Counties, and in the eastern section of Pennsylvania, and further in the Potomac valley at Cumberland and Hancock, Maryland, and Cherry Run, West Virginia. At many of these places highly favorable localities were discovered, but no chimney-builders were found. This is the more convincing since I succeeded with ease in demonstrating the presence of this species on the alluvial flats of the Delaware River in Pennsylvania.

Although our knowledge of the distribution of *C. diogenes* in Virginia and North Carolina is far from being complete, all known localities are on the Coastal Plain, and thus it appears that there is actually a gap in the distribution formed physiographically by the Appalachian system and the Piedmont Plateau.

Our knowledge of the distribution in the west is also very defective, and more particularly we do not know anything about its southern boundary in West Virginia

and Kentucky. Thus it is difficult or impossible to arrive at any conclusion as to its center of dispersal. But at this point certain morphological observations may possibly afford some help. We have seen (p. 407) that in western Pennsylvania the areola is often not entirely obliterated, a condition which is certainly more primitive than the normal one. Such specimens are quite frequent in southwestern Pennsylvania, while in the other parts of the range they are rather rare or entirely absent. This fact, according to Adams' (1902, p. 122, 125) eighth criterion for the determination of centers of dispersal, points clearly to southwestern Pennsylvania. Here the character of the areola is the least progressive, while in either direction from this center, to the east and to the west, it is more progressive. This conclusion is further substantiated by Adams' seventh criterion : "location of least dependence upon a restricted habitat." We do not know much about the "habitat" of C. diogenes in the west and south, but it is certain that in western Pennsylvania it is less restricted than in eastern Pennsylvania. Along the Delaware River I found it exclusively in the black muck of the alluvial flats, while in western Pennsylvania it has a much wider range ecologically, being found in clay bottoms, on hillsides, near springs, swamps, and even on sandy or gravelly soil.

Judging from these facts, and also from the general rule which holds good for the subgenus *Bartonius*, that its center is in the Appalachian region, we may safely assume that *C. diogenes* did not have its center on the Atlantic Coastal plain, nor in the western parts of its range in the Mississippi basin, but that it is somewhere on the Alleghanian Plateau; and since southwestern Pennsylvania and northern West Virginia are the only parts of this plateau occupied by this species, we have to place its center here.

Here, as we have seen, it dwells chiefly upon the late Tertiary base-level of the Old Monongahela drainage, and I believe this was its original habitat. We have no means to decide whether it was already present in this region in late Tertiary times; but the simple fact that it does occupy an area, the physiographical features of which have developed in Tertiary times, is in favor of this assumption. Further on we shall become acquainted with another reason for this view. In the Tertiary period its range very likely extended further north; but the Glacial Period must have restricted it, and its preserve was in the region indicated. In Postglacial times it spread northward again, at least in Pennsylvania. Unlike *C. monon-galensis*, the rivers did not form a barrier, for this species largely descended into the valleys, going down to the river-bottoms and the very banks of the river,⁶⁵ and thus

⁶⁵ It is found frequently on islands in the rivers (Neville and Twelve Mile Islands, near Pittsburgh). 1 have seen chimneys on the river banks near Verona, and obtained specimens on the banks of the Kiskiminetas at Kiskiminetas Junction.

it should have been able to cross the latter. Consequently its range extends beyond that of *C. monongalensis*.

It is doubtful what physical feature constitutes the northern boundary of this species. In Jefferson, Armstrong, and northern Butler Counties, where the boundary is apparently located, the late Tertiary base-level, to which this species belongs, loses its identity. Possibly it was not developed at all, and this region was not reduced to base level. So it might be possible that the roughness of the country constitutes a barrier here, and this is supported by the fact that the boundary is located further south in the Alleghany valley than to the east and west of it. On the plateau-like regions in Indiana and Butler Counties, favorable localities are abundant, while the narrow Alleghany valley, with the deeply cut valleys tributary to it, do not offer congenial conditions.

It is different further west. In Lawrence and Mercer Counties this species has invaded the glaciated area, and is found to the north of the terminal moraine (see Lewis, 1884, p. 183 and 193, Pl. 11 and 12), and here prefers the swampy depressions formed by kettleholes. But a northern barrier at this point is not evident, although a tendency to a northward extension seems to be indicated.

Having thus invaded the area of the drift, it is not astonishing that this species spread over large tracts of the latter in Ohio, Indiana, and Illinois. Its presence to the south of the drift in the Mississippi Valley would then be a continuation of this westward migration, which finally varied toward the southwest and the south. I have represented it as such (Ortmann, 1905*b*, p. 123, Pl. 3) in a previous paper. Nevertheless this question needs further investigation.

There remains the eastern area of this species on the Atlantic Coastal Plain. In the paper just referred to I have expressed the opinion (*l. c.*, p. 123) that it "descended from the mountains" toward the east, but this apparently needs correction. Of course the direct way from its supposed center to the Atlantic plain is from southwestern Pennsylvania and northern West Virginia across the Appalachian system and the Piedmont Plateau to Maryland and Virginia. But the total absence of this species from this region is against this assumption. There is no possible reason why it should have disappeared from the Potomac valley, if it had once been present there, favorable localities being abundant.

Comparing, however, the present eastern range of *C. diogenes* with that of *C. limosus*, we are struck at once by the general similarity. Both species belong to the Coastal Plain from New Jersey southward, *C. diogenes* going a little further south, and not quite so far north, while *C. limosus* has entered the Piedmont Plateau, and *C. diogenes* has not. This similarity induces us to assume a similar

origin of distribution, and in that case *C. diogenes* would also have come from the north, being driven back by the advancing ice.

This necessitates the further supposition that *C. diogenes* is a Preglacial species (another reason for this has been mentioned above), which extended before the beginning of the Glacial Period further north, probably from western Pennsylvania into New York or even beyond. This is not improbable, since the Alleghany Plateau stretched considerably to the north in Preglacial times (see Powell, 1896, p. 80), and although the Preglacial features are largely obscured in this region, it might have been possible for this species to cross over into the coastal plain from western New York to southern New England or northern New Jersey, skirting the northern extremity of the Appalachian system. The coming of the ice must then have resulted in the obliteration of the northern connection of the range, thus dividing the originally continuous area into a western and an eastern subdivision.

According to Adams' classification (1905, p. 58), *C. diogenes* belongs to the *north-eastern biota*, but its dispersal in Postglacial times does not entirely agree with that of the *second wave*. Indeed there is a slight indication of a northward advance in Pennsylvania, Michigan, Wisconsin, and Minnesota, but the main direction was *westward* from the Alleghany Plateau, and even *southward*. This is undoubtedly due to the ecological peculiarities of this species (chimney-builder), it having found no competition in the directions named. In the eastern section of its range a northward advance is hardly noticcable. Here the species is more restricted ecologically (apparently a higher specialization), favoring only the black mud of alluvial deposits, and this very likely prevented its northern expansion. However, its exact distribution in New Jersey is unknown.

8. Summary of the Studies on Geographical Distribution.

We have been able in the preceding studies to advance a theory for the dispersal of each of the Pennsylvanian species of crawfishes. It cannot be denied that in certain points our ideas do not seem to be well supported, but this is chiefly the case in instances where our knowledge of the extralimital distribution is defective. It is to be hoped that similar investigations outside of our state may furnish additional evidence to substantiate our conclusions, or if necessary, to modify them. This much, however, is evident, that the facts of the distribution of our species are due to two causes : (1) partly to the existing physiographical features of the country ; (2) partly to past conditions, which have now disappeared. On the accompanying map (Pl. XLIII), we notice the following particulars. In the eastern part of Pennsylvania, along the Delaware River from Trenton, N. J., to Marcus Hook, Delaware

County, a small part of the Atlantic Coastal Plain enters the state. The Delaware River runs along the escarpment of the Piedmont Plateau ("fall line," See McGee, 1888, p. 122), but at several places a narrow space is left, chiefly opposite Trenton, in Bucks County, and below Philadelphia, where alluvial flats are found. These we may include in the coastal plain, and they are characterized by the presence of *C. diogenes* (together with *C. limosus*).

The next physiographical divisions of Pennsylvania are the Piedmont Plateau and the Great Alleghany Valley, reaching from the eastern escarpment of the former to the Blue Mountain. These divisions form a unit in Pennsylvania. The dividing line between them, South Mountain, being rather insignificant and obliterated, chiefly toward the northeast.⁶⁶ This fact is also expressed to a certain degree in the distribution of the crawfishes. Aside from the generally distributed C. bartoni, we have here C. limosus, which has invaded this region, coming from the lower Delaware, Susquehanna, and Potomac. It seems to have spread all over the Piedmont Plateau, and also into parts of the Great Alleghany Valley, for instance, into the Cumberland Valley (between South Mountain and the Blue Mountain, called here the North Mountain, in Franklin and Cumberland Counties). It has also been found in the Schuylkill and its tributaries in Berks County, but not as yet in the Lebanon and Lehigh Valleys (northeastern continuations of the Great Alleghany Valley). Whether the conditions presented here are original or not seems doubtful. On the one hand it may be that the canals have served to distribute this species; on the other hand, pollution of streams may have restricted it. Be this as it may, the fact remains that the physiographical divisions distinguished as the Piedmont Plateau and the Great Alleghany Valley possess a species of crawfish which is not found elsewhere, except in the Coastal Plain and the Susquehanna Valley.

Then follows the Alleghany Mountain region, between the Blue Mountain and the Alleghany Front (see Willis, l. c.). In the southern and central parts of the state this section is well marked. In the northern part its western boundary is obliterated, the Alleghany Front losing its identity. But all the areas which undoubtedly belong to the mountain region are uniformly characterized by the presence of only the one species, *Cambarus bartoni*, with the exception that *C. limosus* is found in the middle Susquehanna valley from Harrisburg upward to Columbia and Center Counties, and in the Juniata valley up to Bedford County; and further, *C. obscurus* exists in Wills Creek, Bedford County. Both these ex-

⁶⁶See Willis, 1896, p. 172, and map p. 170-171. South Mountain is the continuation of the Blue Ridge of Virginia, while the Blue Mountain of Pennsylvania is not identical with the Blue Ridge, hut is to the west (northwest) of it.

ceptional cases, however, do not represent, in my opinion, original conditions. This is most evident in the case of *C. obscurus* in Wills Creek, where no other explanation is possible except that of artificial introduction. With reference to the occurrence of *C. limosus* in the middle Susquehanna and the Juniata, within the Alleghany Mountains, I think in this case also a recent immigration took place, favored by artificial means (canals). This is, however, somewhat doubtful, since it is impossible at present to ascertain the normal and original conditions prevailing in eastern Pennsylvania before modern improvements were introduced.⁶⁶

The region containing only *C. bartoni* goes beyond the boundary of the physiographical division of the Alleghany Mountains. In the northwest the Susquehanna has captured a large part of the drainage of the Alleghany Plateau, and the whole basin of the West Branch of the Susquehanna is included in the section containing only *C. bartoni*. But again a physiographic boundary is formed by the divide between the Susquehanna and Alleghany river-systems.

All the rest of the state belongs to the *Alleghany Plateau*. Here much more varied conditions prevail with regard to the distribution of crawfishes, and this is chiefly due to the fact that this region was open to Preglacial and Postglacial immigration from the south, southwest, west, and northwest. Aside from *C. bartoni*, which is found everywhere, the following five species immigrated into this region : *C. propinquus, C. obscurus, C. carolinus, C. monongalensis*, and *C. diogenes*. Since each of these species had a different center of radiation, a different geological history, different ecological habits, and since, consequently, different barriers existed to the dispersal, no two species possess the same range.

C. propinquus came from the west and northwest in Postglacial times. It belongs to the Erie basin, and is restricted by the divides of the latter. Thus it is confined in Pennsylvania to the Lake Erie drainage in Erie and Crawford Counties.

C. obscurus belongs to the Preglacial Spencer River or Old Monongahela, and to Lake Monongahela of early Glacial age. The Postglacial dispersal includes first of all the Ohio-Monongahela-Alleghany drainage, and thus generally the divides of this basin constitute its boundaries, with a few exceptions. In the region of the upper Youghiogheny and the Conemaugh the roughness of the streams has prevented it from reaching the plateau to the east of the Chestnut Ridge. In Crawford and Erie Counties it has crossed over into the Erie drainage (due to stream-piracy or to artificial means), and in Potter County it has found a way into the Genessee system (due to stream-piracy).

C. carolinus came from the south, along the high level plains of early Tertiary 66a The green color on the map, Pl. XLIII, should be continued up the Juniata to Bedford County.

age, being partial to extensive clay bottoms. Such conditions are found well developed only between that part of the Alleghany Plateau which is enclosed between the Alleghany Front and the Chestnut Ridge. Possibly also elevation has played a part. Thus it is found only in Somerset and parts of Fayette and Westmoreland counties. The northern boundary is formed by rather insignificant and possibly temporary barriers.

C. monongalensis is a form parallel to C. carolinus. It also came from the south, and invaded southwestern Pennsylvania, keeping to locations of less altitude than C. carolinus. Thus its eastern boundary is formed by the Chestnut Ridge. Its northward advance was checked by the first large river flowing east and west, namely, the Loyalhanna-Kiskiminetas-Alleghany-Ohio.

C. diogenes seems to be similar, at least in western Pennsylvania, to C. monongalensis, but it was able to cross the rivers northward. The northern boundary is obscure, and may be not entirely due to topographical conditions. Attention may be here called to the fact that the isotherms have a curve somewhat similar to that formed by the northern and eastern boundary of this species.

Thus western Pennsylvania is divided into several sections characterized by their crawfish-fauna, namely :

1. Area of *C. carolinus* (containing *C. bartoni* and *carolinus*): Somerset and southeastern Fayette Counties.

2. Area of C. diogenes and C. monongalensis (containing C. obscurus, bartoni, monongalensis, and diogenes): Greene, Washington, northwestern Fayette, western Westmoreland, southern Allegheny, and southern Beaver Counties.

3. Area of C. diogenes without monongalensis (containing C. obscurus, bartoni, diogenes): northern Beaver, northern Allegheny, northeastern Westmoreland, western Indiana, southern Jefferson, southern Armstrong, southern Butler, Lawrence, and southern Mercer Counties.

4. Area of C. obscurus (containing C. obscurus and bartoni): northern Jefferson, northern Armstrong, northern Butler, northern Mercer, the largest part of Crawford, Venango, Clarion, and Forest, western Elk, northwestern Potter, McKean, Warren, and southeastern Erie Counties.

5. Area of C. propinquus (containing C. propinquus, obscurus, bartoni): northern and western Erie and a small part of Crawford Counties.

These are the chief divisions, but there are a few minor differentiations. The greatest variety prevails in Westmoreland County. Its western part (west of the Chestnut Ridge) belongs to two of the above areas (2) and (3), divided by the Loyal-hanna River. But besides the valley between the Chestnut and the Laurel Hill Ridges presents three different conditions, namely:

(a) Conemaugh drainage, with only one species : C. bartoni.

(b) Ligonier Valley, with two species: C. bartoni and obscurus.

(c) Headwaters of Indian Creek, with three species: C. obscurus, bartoni, and carolinus. This latter section also comprises the northeastern corner of Fayette County.

The greatest number of species found in any one county is five, namely, *C. obscurus, bartoni, carolinus, monongalensis,* and *diogenes.* This is the case in Westmoreland and Fayette Counties. They may be found in close vicinity only along the escarpment of the Chestnut Ridge. For the rest *four* is the largest number of species found closely associated, namely the four belonging to the second area, comprising the range of *C. monongalensis.*

In conclusion, attention should be called to the fact that the terminal moraine in no case constitutes a barrier for any of the Pennsylvanian crawfishes. (Compare Lewis' map, 1884, with our maps, Pl. XLII and XLIII.) Of course, for the riverspecies the moraine would not be of any consequence, and of the burrowing species, two, *C. carolinus* and *C. monongalensis*, do not reach it at all, while *C. diogenes* has crossed it in the west. But instead of being a barrier the glaciated area rather seems to offer more congenial conditions on account of the frequency of swampy places (kettleholes).

The question remains, whether our survey of the state is to be regarded as complete and exhaustive, or whether there might be other species within its limits. This is suggested by Faxon (1885*a*, p. 165) as to *Cambarus blandingi* (Harlan). This species is found in New Jersey at Trenton, on the Delaware meadows just opposite the eastern extremity of Bucks County, Pennsylvania, associated with *C. limosus* (Faxon, l. c., p. 22 and 88). I have made a careful search for it in this part of the state, and visited this corner twice (Sept. 15, 1904, and at the same date, 1905). Having collected this species previously in New Jersey, I was acquainted with its ecological habits and knew where to look for it. I indeed found localities that appeared favorable, but I failed to see any traces of the species. I think it is quite safe to assert that this species is not found in this state.

• The case of Lake Erie is a little different. We have records showing that in Ohio the western extremity of the lake is inhabited by *Cambarus rusticus* Girard and *C. immunis* Hagen. The former has been reported from Kelley's Island (Faxon) and from Sandusky Bay (Osburn and Williamson), and from several tributaries of the lake. The latter is mentioned from Lake Érie, off Lorain County (Osburn and Williamson), and from tributaries of the lake as far east as Lorain County. *C. rusticus* is not found anywhere further east, and it seems doubtful whether it finds

congenial conditions *in* the lake. The specimens taken may have been accidentally swept into the lake. Thus I do not believe that it will be discovered in the part of the lake bordering upon Pennsylvania.

C. immunis, however, besides being found in northern Ohio, reappears in New York. Faxon (1898, p. 654) has recorded it from a tributary of Oneida Lake, and recently I have seen specimens, belonging to the New York State Museum, collected by Mr. F. C. Paulmier in Rensselaer Lake, Rensselaer County. Thus its presence in New York, upon which I cast some doubt (1905b, p. 134), is to be regarded as firmly established. However, the connection of these eastern localities with the western range has not been discovered. If a connection is present at all, it is to be looked for in the Erie-St. Lawrence basin, and thus would possibly include the lake shores of Pennsylvania. Yet this connection may not exist, and C. immunis in New York may be a recent, artificial introduction, which is not altogether impossible, since we know that the crawfishes used for food in the New York market come in part from the lake regions (Milwaukee, see Ortmann, 1900, p. 1260), and thus this species may have been introduced. But this question is by no means settled, and we should try to obtain further facts.

Finally we may observe that the conditions now existing in the case of the Pennsylvanian crawfishes may not be original, but may have been altered by human agency. The possible influence of canals upon the dispersion of two species, C. limosus in the east, and C. obscurus in Crawford and Erie Counties, has been discussed in the foregoing pages, and the transplantation of C. obscurus into Wills Creek has been stated to have apparently occurred, accidently or intentionally, through human agency. No other cases of dispersion beyond the natural boundaries by artificial means are probable. But on the other hand certain species may have become extinct, at least in parts of their original range, through human agency. Of this we have many instances, but in our state none has gone so far as to entirely obscure the original conditions. We have pointed out above that the absence of C. *limosus* in the Delaware and Schuylkill Rivers in the region of the Great Alleghany Valley may be due to the pollution of the streams issuing from the anthracite region. That these rivers, as well as the Susquehanna are considerably polluted partly by city sewage, partly by mine-water, is sure (see Leighton, 1903, p. 112, and 1904, p. 48), but whether the absence of C. limosus in this region is due to this fact, or not, cannot be settled.

It is different in the western part of the state. Here *C. obscurus* originally occupied all of the Monongahela and Alleghany drainages west of the Chestnut Ridge, but there are many streams in which it is now lacking, and in which we must assume

its former presence. This is apparently due to the large amount of pollution in these streams, chiefly by water from mines. The pollution of the Alleghany River near Pittsburgh, although bad enough from a sanitary standpoint, and due in the first instance to sewage (Leighton, 1903, p. 122) does not affect the crawfishes, for they are very abundant here, and the Ohio below Pittsburgh is rich in crawfishes. But there are many smaller streams contaminated by the waste of coal-mines.⁶⁷ Such streams are recognized at a glance by the precipitate of reddish and yellowish sulphate of iron upon their bottoms, and are invariably without life. This is most evident in the Monongahela drainage of southwestern Pennsylvania (Washington, Fayette, and southern Allegheny Counties), and also in many smaller streams in Butler, Westmoreland, Indiana, and Jefferson Counties, where coal-mines are abundant. The worst conditions prevail in certain tributaries of the Monongahela, in the Monongahela itself, in the Loyalhanna below Latrobe and the Kiskiminetas, and in Red Bank and Sandy Lick Creeks. The Clarion River is also without crawfishes in Jefferson and Elk Counties, but this is due chiefly to pollution by sewage from wood-pulp mills and tanneries (see above, p. 443). In all these cases it is evident that C. obscurus once existed here, since remnants of it are left at many places in some of the clearer and not polluted side streams. Since this pollution of the streams by coal-mines is bound to increase, C. obscurus certainly will disappear from other streams. As we have seen above it was on the point of dying out in Sandy Lick Creek at Du Bois in 1905 (p. 443, footnote 58). Another case has been observed in Fern-Hollow Run, Pittsburgh. In the fall of 1903 I found a small number of specimens of this species left over in some pools once connected with the run; a sewer had recently been built here, discharging its polluted water into the run. In subsequent years this species was not again seen, and has entirely disappeared, as also from Nine-Mile Run, which receives sewage from Wilkinsburg and Edgewood.

It should be added that *C. bartoni* also is frequently influenced by the contamination of streams, but seems rather more resistant than *C. obscurus*. In two cases this was evident, namely, in Mahoning Creek at Punxsutawney, and in Slippery Rock Creek at Branchton. In both cases the streams were only slightly polluted by mine-water, and contained a certain number of specimens of *C. bartoni*, while *C. obscurus* was absent. The latter existed at Punxsutawney in a pond connected with the stream, and at Branchton in a smaller clear tributary, and consequently must have once been present in the two creeks.

A stream or river polluted in a certain part becomes relatively clear and pure

⁶⁷ As to the chemical processes going on in the so-called "sulphur water," see Leighton, 1904, p. 24.

again further down. This is generally seen in the Ohio below Pittsburgh. Although the Ohio collects all the badly polluted streams of western Pennsylvania, it is itself not unfavorable to crawfish life. The best instance for this is the Cheat River. At Cheat Haven, Fayette County, this river is rather clear and teems with life, crawfishes and *Unionidæ* being abundant. I was therefore astonished at the condition of this river at Parsons, Tucker County, West Virginia. The water there has a foul smell, and is utterly unfit for life, which is due to a wood-pulp mill just above Parsons on Shavers Fork. Between Parsons and Cheat Haven (about fifty miles) the water has improved so far that life is not only possible, but is abundant, only the blackish color of the water remaining as the last result of the contamination.

V. LIFE HISTORY.

Only a few scattered notes have been published on the life-history of any of the American species of *Cambarus*, and some of them are rather doubtful. The most complete account is that given by Andrews (1904) on the breeding habits of *C. limosus*, but even this comprises only a small part of the life-history, and moreover, as may be seen below, is in part rendered unreliable by the fact that the observations were not made in the field, but in the laboratory.

My own observations have been almost exclusively made in the field, and were only occasionally supplemented, or rather confirmed, in the laboratory. Since it was my object from the beginning to watch the behavior of the crawfishes under natural conditions, laboratory-work could not be depended upon, unless controlled by field-work, and thus the former was neglected altogether.

With the exception of January and February,⁶⁸ my work in Pennsylvania extends over the whole year, thus including all seasons. The results are rather satisfactory, and I am able to give a complete account of the seasonal life of no less than four species, and by comparison with these the life-history of the other species of this state may be inferred. Of course I have not been able to solve all questions. For instance the question of the frequency of moulting in one and the same individual remains open, since it can only be settled by observing the same individual continuously; but this is impossible in the field. Nevertheless I have found means to elucidate this question in other ways, although not with absolute accuracy.

The most numerous and most complete records I possess refer to the common river-species of western Pennsylvania, *C. obscurus*, and of this I shall first give an account.

⁶⁸ From New Jersey I possess observations made even in January and February and referring to C. blandingi, C. limosus, and C. bartoni.

1. Cambarus obscurus.

Nothing whatever was previously known in regard to the life-history of this species. I have observed it during the larger part of two seasons, the dates of actual observation covering the time from March 28 to November 19 (in 1904 and 1905).

Beginning in spring (March) it is ascertained that the species is at this time quite active, being found in the usual localities (under stones in rivers and streams), and the specimens are of various sizes and conditions, but all agree in having a rather dirty (mud-incrusted) shell, a sure sign that the shell is old and that no recent moulting has taken place. There are occasional specimens with a very clean shell, in which moulting has occurred quite recently. This teaches us that during the winter months as a rule moulting does not take place, but that it begins quite early in spring, although only in the case of a few individuals. Males of the first form are abundant at this time, while males of the second form are scarce, and it is chiefly these newly moulted males which are of the second form. It seems, however, that in exceptional cases rather young males (30 to 40 mm. long) may have gone through the winter in the second form. The size of the males of the first form varies greatly; the smallest found by the writer in spring (May 2, 1905) measure 40 mm. in length, but specimens between 40 and 50 mm. long are very abundant. All the males between 30 and 40 mm. long are of the second form, but they are not abundant, as has been stated. The smallest male found in spring was 31 mm. long. The condition of the females in early spring corresponds to that of the males, and in this sex the minimum size is 27 mm. in length.

Very soon an important event takes place in the life of the females. Eggs are laid. No signs of this were seen on March 28, 1905, and March 31, 1905, although a large number of individuals were collected at these dates. But on April 6, 1905, (in Thorn's Creek, Renfrew, Butler County), numerous specimens with eggs were taken, some in the very act of spawning. I was able to observe in this species the peculiar attitude assumed by the female, and the "apron," described by Andrews for *C. limosus* (1904, p. 180, fig. 5; p. 182, fig. 6). The same was seen repeatedly on subsequent dates in April, so that April is to be considered as the spawning season. The number of eggs is rather large, one hundred to two hundred and even more, but young specimens sometimes have considerably less.

From the beginning of April onward females with eggs are found very regularly until the end of May. My dates are the following: April 6, 1905; April 10, 1905; April 19, 1905; April 24, 1905 and 1906; May 1, 1905; May 2, 1905; May 3, 1899 (Williamson and Shafer); May 4, 1905; May 8, 1905; May 17, 1906; May 22, 1905; May 25, 1905. With one exception (April 15, 1905) I found females with

eggs every time I collected this species during this period. This rather precisely fixes the time when the females are "in berry." They carry eggs during the months of April and May, but at no other time of the year, and during this season all females, with few exceptions, no matter whether they are large or small, have eggs. The smallest observed with eggs was 40 mm. long. Of course in the beginning of the spawning season larger females may also be without eggs, but later on females larger than 40 mm. long are only very rarely found without them. The latter generally are newly moulted (having soft or clean shells), showing clearly that at the beginning of the spawning season they were very likely below the minimum size for spawning. Of the few females under 40 mm. long none had eggs.

During the spawning season (April and May) a general tendency toward moulting is observed in all specimens which are not females "in berry." Among the sterile females, as well as among the males, the old, dirty shells disappear; newly moulted shells become more and more frequent, and soft shells are frequently observed. This moulting process in most individuals takes place in the first half of May, but, as we have seen, some individuals begin as early as March, and in others the process is delayed till the beginning of June. But by this time all specimens have moulted under normal conditions, with the exception of the fertile females, which moult after the young are hatched in June.

A remarkable fact in the case of the males is that this spring moult invariably changes them to the second form.⁶⁹ In consequence males of the first form become scarcer and scarcer, till finally at the beginning of June all have disappeared and only males of the second form are left. Another remarkable fact is that after the end of the moulting season in spring no very large males are found. While large males of the first form of over 70 and 80 mm. in length are quite abundant in March, April, and the first half of May, they become very rare after that time, and the males of the second form, which are then abundant, only in rare instances exceed the size of 70 mm. in length, (only two cases on record). During the summer the males are generally less than 70 mm. in length. Large males reappear after the summer and fall moults begin, and then they are again of the first form.

The question arises what becomes of the large males (over 70 mm. in length), which are rather frequent in spring. According to the records, we cannot assume that they moult into the second form, for we should then find large males of the second form in summer. Thus it is suggested that these large males die and disappear. Of this I have found positive evidence in two cases. On June 6, 1904, I collected in the Shenango River at Linesville, Crawford County, a large male of the first

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⁶⁹ This change was first observed by Faxon (1884a, p. 42) in Cambarus rusticus Girard.

form, 81 mm. long, which was lying concealed under a rock in the usual position. It was absolutely perfect, without blemish, and with an old, very dirty shell, thus clearly showing that it had gone through the previous winter. This specimen was barely alive and to all appearances in a dying condition. A similar instance was noticed on April 24, 1905, in Wheeling Creek, Elm Grove, West Virginia. Here a large male of the first form (84 mm. long) was found showing no signs of injury, in fact in very beautiful condition, but barely able to move. It was kept in water, but was dead the next day, while other specimens collected together with it were none the worse for their journey to Pittsburgh. Thus it seems that the conclusion is justified that the largest males of the first form, after having in the autumn attained a certain maximum size, which may be different according to conditions, but may be said in general to be about 80 mm. in length, go through the winter, but do not moult again, and die a natural death in spring.⁷⁰

The latest dates at which I found males of the first form in spring are as follows: June 6, 1904, Linesville (the case just mentioned), May 30, 1904, at Waynesburg, Greene County; May 25, 1905, Alleghany River, Mosgrove, Armstrong County. After the beginning of June, all through the month, and through a large part of July, no males of the first form have been found, and through the remainder of July they are scarce. (See below.)

The eggs carried by the females hatch at the end of May and the beginning of June. I found young under the abdomen of the mother on May 30, 1904, on June 5, 1906, and on June 6, 1904. The period during which the young stay with the mother seems to be short. On May 25, 1905, I found eggs, not yet hatched. From June 15, 1905, onward all through the remainder of the year I never observed a female with eggs or young. Between these two dates I have only four records, May 30, 1904, June 2, 1905, June 5, 1906 and June 6, 1904, in three of which the presence of young ones with the mother was shown. Thus the period when young are found under the abdomen of the mother is very likely the end of May and first half of June (about three weeks), and the young crawfishes probably do not remain with the mother much longer than a week.

Throughout June and part of July no males of the first form are present; all males are of the second form, but they are not very large, reaching a maximum size of only between 60 and 70 mm. The females have got rid of their progeny, and begin to moult. The old females may die like the old males, but I have no evidence on this point, except as drawn from analogy to the males, and the fact that

¹⁰ A great mortality of males in spring (after copulation in captivity) has been observed by Andrews (1904, p. 175) in C. limosus.

very large females are rare in the latter part of June and in July, and do not become more abundant till the beginning of August. In addition we now have a new generation of young crawfishes, hatched at the end of May and beginning of June. After these have left the mother it is difficult to get them. They are too small, and are often overlooked, and if captured in the net, are able to escape through the meshes. But I have seen them at this time, although the first recorded captures are as late as July 10, 1900 (by Dr. D. A. Atkinson), size 26 mm., and July 24, 1905 (by myself), size 21 to 23 mm. This young generation is easily distinguished from the rest by its size, being considerably less than 30 mm. in length. The minimum length of crawfishes in spring is 31 mm. in the case of males and 27 mm. in that of females.

In the middle of July further changes occur. A new period of moulting begins for the medium-sized and older individuals, which is chiefly noticeable among the males, since they now again assume the first form. The earliest date for the new males of the first form is July 11, 1905 (Tionesta and Spartansburg). Altogether four individuals were taken, all of which had soft shells, showing the fact that they Further dates are July 24, 1905 (Deer Lick), July had recently moulted. 25, 1906 (Russelton), July 26, 1904 (Derry), July 27, 1906 (Shousetown), and then in August and the following months they regularly occurred. At first these males of the first form are scarce, but they become gradually more frequent, till finally at the end of September and in October almost all males have assumed the first form. This also holds good for the new generation born at the end of May and the beginning of June. These young ones are about 20 to 23 mm. long in July; in August I have specimens from 24 to 39 mm. in length; in September from 26 to about 50 mm. in length. About this time this generation becomes obscured; for it seems that the rate of growth of the young crawfishes is very different in different individuals, some gaining during June, August, and September, only about 15 mm. in length, others more than twice that length. They are about 10 or 11 mm. long when they hatch. The same fact was observed by Andrews (1904, p. 202) in C. limosus, with even greater differences in size (the length of the young of the same generation in October being between 22 and 60 mm.).

It is ascertained from the above observations that young specimens, born in early summer, already at the end of the first summer (September and October) reach a size sufficient to prepare them for propagation, and the males of this generation as a rule show this by changing into the first form. The smallest male of the first form, collected by myself in fall (October 6, 1905), is a specimen from Kittanning, 38 mm. long, but specimens from 40 to 50 mm. long, and undoubtedly belonging to this generation, are quite abundant at this time. Thus we see that by October

the same conditions are established which were found in early spring. Males of the first form prevail, and those of the second form are scarce, and generally of a small size, between 30 and 40 mm. long. Specimens of less than 30 mm. in length are very rare and represented by individuals of the last generation, which have not been able for some reason to keep pace in growth with their brothers and sisters. The males are sexually mature, and apparently the females likewise, as we shall presently see.

Copulation actually takes place now. 1 have quite often observed it in the field; and made record of the following dates: September 5, 1906; September 28, 1905; October 6, 1904; November 19, 1904. In addition couples were found apparently preparing for copulation, but not in the act, on September 7, 1905, and September 30, 1905. Among the material collected by Mr. W. R. McConnell was a couple taken in copula on September 5, 1905. In captivity I observed copulation on September 8, 1905, and November 22 and 23, 1904, and I have found that it is very easy to induce couples to copulate about this time (September, October, November), provided that one male and one female are put in the same jar. In no other part of the year, and, what is more important, not even in spring (March, April, May) does copulation take place, either in nature, or in the laboratory. All my attempts to induce specimens to copulate in spring have been in vain, and, of course, in June, July, and part of August, copulation is impossible, the males not being in condition. Copulation may occur in August, males of the first form being present, but possibly the females are not in proper condition before September on account of the delay of the spring moult. The smallest female seen in copulation was 43 mm. long; and she undoubtedly belonged to the generation born in spring, thus establishing the fact that the females like the males are generally sexually mature at the end of the first summer, and that they are able to produce eggs the next spring. (See above. The smallest female with eggs was 40 mm. long.)

The above observations and conclusions are founded upon the comparison of large numbers of individuals, but no single specimen has been followed through all the different stages of seasonable development. But to a certain extent it is possible to ascertain the changes through which one and the same individual has to go, and to lay down its life history.

The young *Cambarus obscurus* is hatched at the end of May or the beginning of June, from eggs laid in April. The young stay with the mother under the abdomen of the latter, for a short time (about a week); then they shift for themselves and develop during the summer rather quickly, inoulting repeatedly.⁷¹ In Septem-

⁷¹ Compare Andrew's observations on C. *limosus* (1904, p. 190, ff.) : he distinguishes seven larval stages (each beginning with a moult), from the hatching, end of May, to the middle of July, when a length of 29 mm. was reached.

ber or October they have attained a length of from 40 to 50 mm., and the males have assumed the first form. The females also are sexually mature, and *copulation* takes place from September to November.⁷² During the winter no changes occur, and in early spring they are in about the same condition as in the previous fall. In April the females *spawn*, and it is remarkable that spawning takes place normally from four to six months after copulation. The males generally go through the *spring moult* in May, the females a little later in June. This brings up the size of this generation to from 50 to 60 mm. Then the *fall moult* begins, lasting from August to October, in which the specimens attain a size of over 60 mm. After the first summer only two moults, the one in spring and the other in fall, seem to take place.

At about this time, (October of the second year), the specimens are seventeen months old. They go through a *second copulating season*, and through the following winter, and again through the spring and summer with the same changes, attaining by the two moults their maximum size of over 70 mm. in length. A *third copulating season* follows, their age being now two years and five months. After this they live until the next spring, when the old males die in April and May, and the old females probably in June. This shows the life of the individual to be about three years.⁷³

This seems to be the usual life-cycle of this species. But there are exceptions, which are primarily due to the fact that in the first summer the growth of single individuals may be quicker or slower. Whether slow growth, inducing late develment, influences the total length of life cannot be ascertained, but it must lead to the result that some specimens are not sexually mature at the end of the first summer, and that thus the first copulation is postponed a whole year; for copulation seems to depend directly on the season, and takes place exclusively in fall, but never in spring. Furthermore it may be that in single cases life is prolonged an additional year, as for instance in exceptionally large individuals (about 90 mm. long). But we may safely assume that three years, or at the outside in exceptional cases four years, is the duration of the life of this crawfish, and that an individual that lives up to this age without having met with an accident has fulfilled its destiny and dies a natural death.

A few additional remarks should be made with reference to egg-laying, moulting, and copulation. The act of laying eggs is hard to observe, and I cannot improve upon Andrews' observations on *C. limosus* quoted above. The process of moulting,

⁷² Possibly beginning at the end of August and extending to January.

⁷³ Andrews (1904, p. 204) was able to trace *C. limosus* only to the third summer, when the sole survivor of his material reached the size of 90 num.

is also rarely observed. The old skin splits on the back, between the carapace and the abdomen, and the crawfish pulls itself out gradually, leaving the empty shell intact. I have not made any observations on the increase of size at the moulting time, in the case of this species. (But see below under *C. diogenes, monongalensis*, and *C. bartoni*.) None of my specimens kept in captivity went through this process, and those found in the field immediately after or during the act were too flabby to be measured. Empty shells have been found now and then, but the individuals belonging to these had then lost their identity. Possibly, as has been observed in *C. monongalensis*, the old shells are eaten up.

The copulation resembles throughout that of *C. limosus*, as described by Andrews (1895, p. 867, and 1904, p. 166, Fig. 1, p. 168), and only a few remarks seem necessary. The male with its claws takes hold of the claws of the female at the base of the hand or the base of the fingers, and in shifting its position it often seizes several of the other pereiopods of the female. The other legs of the male are lying on the sides of the carapace of the female. All the legs of the female are lying close together on each side, directed forward. The male uses one of the fifth pereiopods, sometimes the right, sometimes the left, to elevate the copulating organs, and this leg is laid across the sternum, sticking out on the other side behind the fourth pereiopod. The use of the hooks is the same as in *C. limosus*.

After copulation the annulus of the female contains a "spermal plug," as described in *C. limosus*. Copulation takes place repeatedly between the same couple, and one male may copulate in succession with several females, and one female with several males. This has also been observed by Andrews (1895, p. 867) in *C. limosus*, who says copulation "may be repeated by either animal with some other."

2. Cambarus propinguus and Cambarus propinguus sanborni.

My observations on these two forms are fragmentary, but the dates at hand make it certain that the seasonal history is identical with that of *C. obscurus*.

For *C. propinquus* I have only three observations dated in the summer; the most important being June 7, 1904 (Conneautville Station), when I collected a considerable number of this species. As in the case of *C. obscurus* no males of the first form were found, and all males of the second form as well as females were of medium size, between 47 and 60 mm. long. Specimens collected at the end of August, 1900, by Dr. D. A. Atkinson at Presque Isle were in the same condition (no males of first form), but there was with them a young female 27 mm. long, belonging apparently to the generation born in June.

The rest of my material was collected on October 4 and 5, 1904, in Erie County.

Here males of the first form were abundant. while those of the second form were few and small (between 32 and 43 mm. long). The latter consequently all belonged to the generation of that year. Some of them very likely would have changed into the first form within a short time. The smallest male of the first form was 39 mm. long.

In addition I have seen specimens from Lake Erie, Lorain County, Ohio (Oberlin Museum) collected May 1, 1892, which demonstrate the presence of males of the first form in spring, and I have received from Mr. E. B. Williamson a couple collected September 1, 1901, in Emmet County, Michigan, in the act of copulation. The date is slightly ahead of my earliest date for this act in *C. obscurus*, but falls into the same general season. All these dates perfectly agree with the rules laid down for *C. obscurus*.

Of *C. propinquus sanborni* I have collected material only in the early spring and late summer. The specimens observed in spring (April 14 and 28, 1905), in the Tuscarawas drainage, Ohio, correspond entirely to the spring condition of *C. obscurus*. Generally they have a thick coat of dirt, showing that they have gone through the winter without moulting. Most of the males are of the first form, but a few are of the second form, and these have new shells. A large number of the females have eggs. From Dr. Sterki I received a number of newly hatched young, 12–15 mm. long, collected on June 18, 1906, at Dennison, Tuscarawas County, Ohio. Among the specimens collected on August 28 and 29, 1905, in Wetzel and Pleasants Counties, West Virginia, many males of the first form were present, but also a considerable number of the second form ; besides, there were a number of small specimens of the generation of that year. Among the material of this form from Oberlin, collected September 28, 1903, the same was true, and thus in this form also the known facts agree with what has been observed in the case of *C. obscurus*.

3. Cambarus limosus.

This is the species on which Andrews (1895 and 1904) made his observations. My own dates, which are supplemented by those collected by Mr. H. Gera and Mr. W. R. McConnell, are comparatively few, but, as far as they go, show certain discrepancies with Andrews' results, which need attention and explanation.

The largest number of observations I possess are dated in the month of September, when I collected this species at numerous localities in eastern Pennsylvania, New Jersey, and eastern West Virginia in the years 1898, 1904, and 1905. At this time the condition of this species entirely corresponds to that of *C. obscurus*. Males of the first form are abundant and of all sizes. (Smallest, 37 mm. long, from Stony Brook, Princeton, New Jersey, September 21, 1898, and 40 mm. long, from Gren-

oble, Bucks County, Pennsylvania, September 20, 1904.) Males of the second form are scarce, and most of them are of small size (between 28.5 and 40 mm. long). Among the females also are many small individuals (as small as 25 mm. long). These small specimens clearly belong to the youngest generation, born in the spring of the year of capture.

Copulation was observed by Mr. H. Gera on September 4, 1905. I saw a repeated copulation of the identical couple on September 10, 1905, and again, in other specimens sent to me alive by Mr. Gera, on November 4, 1905. In addition I have seen this species copulating in captivity in the Anatomical Laboratory of Princeton University in January, 1899, (Ortmann, 1900, p. 1242). Thus the copulating season is identical with that of *C. obscurus*, and lasts from September into the winter, possibly January.

C. limosus goes through the winter,⁷⁴ and is found in spring in the same condition as in fall (April, 1899, at Princeton). In May I found females with eggs (May 9, 1905, Potomac River, Cumberland, Maryland), and on May 30, 1898, I collected females with young under the abdomen (Stony Brook, Princeton, New Jersey). Thus the spawning season seems to be identical with that of *C. obscurus*. During a part of the summer males of the first form seem to be absent. I record that in July, 1904 (specimens collected by H. Gera in Camden County, New Jersey, without exact date), no males of the first form were found. In a large set preserved in the Academy of Natural Sciences of Philadelphia, collected by H. W. Fowler in the Delaware River at Holmesburg, Philadelphia County, on July 4, 1899, all the males are of the second form, and this although there are specimens in this set over 80 mm. long. Among the collections of W. R. McConnell there is a set of this species taken on July 10, 1905, at Milesburg, Center County, which contains two males of the first form, with quite fresh shells. This date corresponds closely to the first date (July 11), at which males of the first form of *C. obscurus* were observed.⁷⁵

According to the above records it seems very likely that the seasonal history agrees in every particular with that of *C. obscurus*. The mating season in fall, the spawning season in spring, and the absence of males of the first form in early summer (June and part of July) agrees with what we know of *C. obscurus*. Comparing this with the account given by Andrews, we find the following differences.

⁷⁴ I collected specimens in January, 1899, in the Delaware-Raritan Canal, near Princeton, New Jersey. All the males were of the first form. Collecting was done by seining under the ice. The crawfishes were obtained in water about four or five feet deep.

⁷⁵ Mr. McConnell collected a newly moulted male with a soft shell, of the first form, at Bloomsburg, Columbia County, on July 19, 1905, and during August he has several dates for these males : August 10 (Reading) ; August 18 (Marion) ; August 21 (Greenpark) ; August 22 (Landisburg).

Andrews (1904, p. 166) places the normal mating season in the months of February, March, and the beginning of April, and says that there seems to be an autumnal pairing (October, November) "in place of or in addition to" the spring pairing. I believe, however, that the autumnal pairing is the normal one, which may be extended through the winter. Indeed I have observed it in January, but only in specimens kept in captivity. Since Andrews' observations were made in the laboratory, it appears probable that the mating may be continued or repeated under exceptional conditions such as are offered in captivity, but that this is not normal. In *C. obscurus* I am positive that under natural conditions copulation does not take place in March and April.

The time of spawning, as observed by Andrews (1904, p. 176) agrees well with our records (end of March and April), also the time of hatching (*l. c.*, p. 187), late in May.

As to sexual maturity, Andrews did not gather facts to show that females are mature and oviposit at the end of the first year (1904, p. 206), although he observed copulation at the end of the first summer. I observed, on November 4, 1905, copulation taking place in specimens less than 45 mm. long, and found females "in berry" of the size of 50 and 45 mm. (Cumberland, May 9, 1905). Since the same fact has been observed in the case of *C. obscurus* it is certain that males as well as females are sexually mature at the end of the first summer, and that the sexual union is effective, the females spawning the following spring. However, in such small females the number of eggs is generally very small (fifty or less).

Thus it seems that *C. limosus* agrees perfectly with *C. obscurus* in its life-history, and that the only marked difference from Andrews' account concerns the mating season. This is however apparently due to the fact that Andrews' observations were made in the laboratory. The explanation for this is very likely to be sought in the temperature conditions. The water used in tanks in laboratories has generally a rather uniform temperature throughout the year, while under natural conditions the temperature of ponds, rivers, and streams varies considerably in summer and winter. I made a few observations with reference to *C. obscurus*. In January, under the ice, the water is near the freezing point, say about 35° F.; on April 6, when females were found spawning, the temperature of Thorn Creek, Butler County, was 45° F. On May 1 the temperature of Grave Creek, Marshall County, West Virginia, was 66° F. and spring moulting was going on. In midsummer I observed a temperature of 82° F. in Bates Fork, Greene County, on July 24, and a temperature of 78° F. in the Ohio, at Ambridge in Beaver County on August 24.

This gives a range of from about 35 to 80 during the year, and I have no doubt

that the nice restriction of certain periods in the seasonal history is primarily due to differences of temperature. It is only natural that an equalizing of the temperature must tend to efface the seasonal periods.

4. Cambarus diogenes.

According to my observations, which extend over the period from March 22 to November 17, this species also agrees in the main features of its seasonal development with *C. obscurus*.

I have the following records for females with eggs: April 6, 1905; April 19, 1905; May 2, 1904; May 14, 1899, (collected by Atkinson, Graf, and Williamson); May 21, 1906; May 22, 1905; May 27, 1904. On May 21, 1906, and June 2, 1905, I found several females with newly hatched young under the abdomen. In no other part of the year has this been observed, and thus the spawning and hatching season is well fixed (April, May, and the beginning of June), and is found to be identical with that of *C. obscurus*.

The number of eggs is considerably less than in the case of C obscurus, and generally falls considerably short of one hundred. The spawning does not take place outside of the burrows, but inside of them, and this was most evident in a female collected on April 6, 1905, (Renfrew, Butler County), in which the eggs were quite fresh, with traces of the "apron" still visible. This female was dug out of its hole, as were all the rest with eggs or young ones.

After hatching the young remain a short time under the abdomen of the mother. But soon they leave her, yet remain in the same hole. I have repeatedly found young specimens in the same hole with their mother, namely, on June 13, 1904; June 15, 1905; July 6, 1905; July 19, 1905. The smallest were about 10 mm. long. These young specimens generally occupy a separate part of the burrow, and are often found near to and inside of the mouth of a closed chimney. They remain in the hole until they attain a length of 20 mm., which happens toward the end of July. Then they leave the hole of the parent crawfish and begin to build their own little holes and chimneys. I observed this on July 26, 1904, at Derry, Westmoreland County, when I discovered a female 20.5 mm. long in a small hole of its own. At the same date I found a larger one, 30.5 mm. long, which may have belonged to the same generation. On August 4, 1904, at Francis Mine, near Burgettstown, Washington County, I found numerous young specimens between 20 and 29.5 mm. long, all in their own holes. On August 22, 1905, at Squaw Run, Allegheny County, I discovered two young specimens 22 and 28 mm. long. On August 26, 1905, at Baden, Beaver County, specimens 31.5 to 42 mm. long were found apparently under

the same conditions. As late as September 5, 1904, (Smithfield, Fayette County), and October 6, 1905, (Kittanning, Armstrong County), I found two very small specimens (24 and 20.5 mm. long) in small holes. Never after July 19 have I found young ones in the hole of the mother, so that it is quite sure that at the end of July they invariably shift for themselves when they have attained a length of about 20 mm. The largest found in the hole with its mother was 18.5 mm. in length, on July 19, 1905. Since young specimens found in the same hole, apparently being brothers and sisters, often have a different length (15 to 18.5 mm. in the case just mentioned), and since, as said above, specimens of only 20.5 mm. in length are found as late as October, the rule is established in the case of this species also that the individuals of the same litter grow up at a different rate.

With regard to the presence of males of the first form, the same conditions seem to prevail as in the case of *C. obscurus*. These males are frequent in spring. I found them at the following dates: March 23; April 2, 6, 15, 16, 24, 30; May 2, 3, 13, 14, 21, 22, 27, 29; June 2, 15. Then follows a gap of over a month to July 20. Within this period I made observations upon the following dates: June 16, 18, 26, 27; July 6, 16. At none of these dates did I discover a male of the first form. It is true that the material in this species is less abundant, a dozen specimens collected on one day representing a rich haul; but it is nevertheless remarkable that during the period just mentioned, in which particular pains were taken to get males of the first form, none were secured. But after this they again appeared regularly, namely: on July 20; August 7, 8, 22, 26; September 5, 7, 15, 19, 21; October 6, 9, 11, 18, 24; November 5. This makes it evident that in early summer (end of June and beginning of July) there is a time when no males of the first form are present.

However, males of the second form are found at any time in the year as frequently as those of the first form. In this respect *C. diogenes* seems to differ from *C. obscurus.* This seems to be due to the fact that *C. diogenes* attains sexual maturity at a later age than *C. obscurus* and the river species in general. The smallest male of the first form ever found measures 55 mm. in length (August 22, 1905, Montrose). It is hardly possible that this individual should belong to the generation born in June of the same year, since the latter are known to be at that time about 30 or at the utmost 40 mm. long. We may assume that *C. diogenes*, like *C. obscurus* and *C. limosus*, may attain at the end of the first summer a length of about 40 or 50 mm., but these individuals do not then assume the first form as the river species do. The same is true of the females. The smallest seen in copulation (or associated with a male) was 63 mm. long, and the smallest female with eggs was 62 mm. long.

Young specimens less than 30 mm. long have not been found in spring, with one exception, when a female of 25.5 mm. in length was found on May 27, 1904, at Squaw Run. This, however, apparently was an exceptionally delayed individual of the generation of the previous year. It was found under unusual conditions, under a stone on the banks of the creek, evidently removed from its original habitation by winter or spring floods. No additional specimens were seen in close proximity.

I cannot say much in the case of *C. diogenes* in reference to the regular moulting periods which were observed in *C. obscurus* to take place in spring and fall. I have repeatedly found soft shells, and on April 24, 1904 (Nine-Mile Run, Pittsburgh), at a place where a large colony of this species was present, I picked up numerous cast-off claws,⁷⁶ which would indicate an early spring moult. But these claws may have accumulated during winter and spring. The rate of increase at a moult was measured in one instance. A female, 52 mm. long, captured on April 6, 1905, was kept in captivity, and moulted on July 16. After this process it was 54 mm. long. This cannot be regarded as entirely normal, since the specimen was kept under unfavorable and artificial conditions.

The copulating season of this species also falls in the autumn. I have only twice observed a male and female in copulating attitude, but in both cases they let go when disturbed. This was on November 5, 1904 (Nine-mile Run, Pittsburgh), and on October 24, 1905 (Branchton, Butler County). The first couple was found in water inside and near the mouth of a comparatively simple hole. The male was 70 mm., the female 81 mm. long. The second couple was found a little deeper, but not over a foot, also in water. The male was 64 mni., the female 63 mm. long. Mr. F. E. Kelly reports a similar observation made by him on November 14, 1904. Besides on two other occasions I found males and females associated in couples in the same hole. Three cases were observed on September 5, 1904, at Smithfield, Fayette County, and two cases on August 26, 1905, at Baden, Beaver County. Since it is an absolute rule that under ordinary circumstances only one specimen occupies a hole, these finds are significant, and, inasmuch as in all these cases it was always a male of the first form which was associated with a female of good size (over 63 mm. long), it is evident that this association was connected with the mating process. Whether the male visits the female, or vice versa, I do not know. In every case the pair was easily captured, being lodged not far from the entrance of the hole. In some of these cases I was struck by the simple character and small depth of the burrow, and it may be that the couples dig out small, temporary holes

⁷⁵ After moulting the shell is generally eaten up, with the exception of the big claws.

for the mating time. This, however, needs further investigation, and possibly, if found to be the case, may, nevertheless, not be the general rule.

In no other part of the year were similar observations made, and this fixes the mating season for the months of August, September, October, and November,⁷⁷ agreeing with what we have observed in the case of *C. obscurus*.

Thus we see that the seasonal cycle in the life of C. diogenes corresponds closely to that of the river-species. The only difference is in the time when sexual maturity is reached, and it seems that in the case of C. diogenes this does not occur earlier than at the end of the second summer. Whether this influences the duration of life is not known. Nevertheless the fact that this species frequently, or even regularly, reaches a size superior to that of C. obscurus, specimens of over 90 mm. in length being quite often found, suggests that this crawfish may live more than three years, possibly four or five.

The resemblance of the life-history of this burrowing form to that of the river species is due, I believe, in large part to the similarity of conditions of temperature. As has been stated, *C. diogenes* lives near stagnant water and swamps, in places where there is generally not much fresh and cool water, although such places are not strictly avoided, and where the temperature of the water is subject to considerable seasonal changes. In winter and spring the water in the holes is rather cool (43° Fahr. on March 23, 1905, in Nine-Mile Run), while in midsummer it becomes when stagnant, almost lukewarm.

The above observations are in part at variance with those made by previous writers on the same species. Girard (1852, p. 88), near Washington, D. C., found females with eggs in March and April, which agrees with our dates, making allowance for the difference of climate between Washington and western Pennsylvania. Girard also noticed the fact that as a rule only one individual was found in each hole and mentions as an exception that in one burrow a male and a female were found together. However, he neglects to tell the exact date of this find (his observations were chiefly made in spring). In one case, he says that a male was seen walking over the surface of the ground, as he believes, in search of the female. But in this instance also no date is given.

Tarr (1884, p. 127) never found male and female together (in May, near Washington), and always only one individual in each burrow, and he never found specimens outside of the holes.⁷⁸ He further believes that the burrowing crawfishes re-

⁷⁷ It possibly extends further into the winter, as in the case of the other species discussed.

⁷⁸ Although I have myself never seen a specimen of *C. diogenes* walking over the ground, this must sometimes occur, for males and females must come together in the mating season, and the holes do not communicate underground. According to Williamson (1901, p. 12), *C. diogenes* and *C. monongalensis* are nocturnal, and that they come out of their holes at night is shown by the fact that Mr. Rhoads captured some of them in traps set out over night for rodents.

treat to the streams in the winter, and in spring construct holes for the purpose of rearing their young, and that impregnation takes place after the winter has passed. These ideas are not supported by any evidence, and are, as we have seen above, incorrect. His opinion that the same burrow is not occupied for more than one year is also not supported by our observations. The time of hatching of the eggs is given as about the middle of May (p. 128), which agrees with our dates. Faxon (1885a, p. 74) reports that according to Mr. P. R. Uhler the female during the period of incubation goes into pools, ditches, etc. This, however, is contrary to the observations of Girard, Tarr, and myself. All these particulars refer to the eastern form of *C. diogenes*, on the coastal plain, and it seems that with regard to the spawning season and the spawning habits this form agrees with that of western Pennsylvania, always considering the slight difference in climate which makes this season begin a little earlier in the Atlantic lowlands.

The observations made on the western form show more marked differences. Bundy (1877, p. 171) reports the discovery of a female with eggs nearly ready to hatch, near Mechanicsburg, Henry County, Indiana, on January 1, 1875. Hay (1896, p. 491) found that the breeding season in Indiana is in early spring, and observed copulation on April 2, 1892. At this time the specimens leave their burrows, and are frequently found in open ditches and streams. The eggs were laid from April 18 to April 30. He also repeatedly saw females with well grown young in small streams. According to Harris (1890, p. 267) a female with eggs was found in Kansas on May 3, 1891,⁷⁹ apparently in an open ditch, as is shown by the subsequent sentences.

With the exception of Bundy's record these dates show April and May to be the normal spawning season of the western form also. The observations of Hay and Harris, that *C. diogenes* frequents open ditches in spring, and that it copulates in spring, are, however, entirely at variance with the habits of this species in western Pennsylvania. This is not the case here, and I have never seen specimens outside of their holes in spring. My observations began as early as March 23, at a time when the frost was hardly out of the ground.

That this is also not the general rule in northern Indiana is shown by notes sent to me by Mr. E. B. Williamson from Bluffton, Wells County, Indiana. Mr. Williamson writes to me : "As to *C. diogenes* congregating in ditches and the like in spring I have no evidence here. The large males of *diogenes* can be expected in almost every little stream. They move about on the bottom restlessly, not lying concealed. Often the current catches them and they roll over and over, but they

⁷⁹ Sic. Note the discrepancy between this date and the date of publication.

always keep moving. *Diogenes* also wanders across country at this time, in daylight as well as at night. I have found several crushed in wagon roads. *Under* these circumstances I have yet to find a female." In another letter Mr. Williamson says pertinently that the specimens taken by him in spring in open ditches are all old males, "in which the death instinct had developed."

Thus it seems evident that the western form does not agree with the form found in Pennsylvania in so far that in early spring the specimens seem to habitually leave their holes. Whether it is only old males when about to die (analogous to what we observed in the case of *C. obscurus*) which wander about, or whether the females with eggs also are found in open water, and further, whether copulation normally takes place in spring, are assumptions which remain to be proved. The observations of Bundy, Hay, and Harris are surely correct, but it remains to be ascertained whether they represent exceptional cases, or whether they are the rule. Moreover it is not improbable that in the western form the seasonal cycle is slightly different, since it lives under somewhat different surroundings. Hay (1896, p. 491) reports that during the dry months of the summer *C. diogenes* seems to lie at the end of the burrow (which contains hardly any water) in a sort of a stupor. I never observed anything like this in Pennsylvania, the holes of *C. diogenes* being always well filled with water at the bottom, and the crawfishes being very lively.

That observations on the habits of this species should always be considered carefully with reference to all accompanying facts is evident from the following case : Dr. D. A. Atkinson found a number of specimens on April 20, 1905, in open pools near Westview, Allegheny County, Pennsylvania, in a region where this species is abundant. These pools were in the course of an old, abandoned mill-race, which dried out late in summer. All these specimens, seven in number, were young, measuring from 33 to 52 mm. in length, and consequently belonging to the generation of the previous year. Now, bearing in mind the fact that the late summer and fall of 1904 and also the winter of 1904-5 were characterized in our region by an extreme lack of precipitation so that all streams were exceptionally low till the middle of March, 1905, when a flood (March 20 to 25) restored the normal conditions, it is very likely that this mill-race was dry in the summer and fall of 1904, when these young specimens began to make their own burrows. They selected this place as a favorable one, and remained there all through the winter, a few smaller floods, one on January 13 and another on March 9, not disturbing them, till the big flood filled the mill-race again for a longer time, Such conditions, however, do not suit this species, and consequently the specimens came out of their holes, and were found, at least for a time, in the open pools, till they had selected more convenient

locations in the neighborhood. Thus this case must be regarded as exceptional, not as a regular or normal episode in the life of the species.

5. Cambarus bartoni and Cambarus bartoni robustus.

In all the species discussed so far we have found a regular seasonal period in the life-history, marked chiefly by a distinct mating-season in fall, a spawning-season in spring, and a season in early summer when no males of the first form are present. But it is entirely different in the case of *C. bartoni*. In this species none of these seasons is recognizable.

As to the mating period, I have observations on only two dates. On May 27, 1904, I found a couple *in copula* in Squaw Run. Here I was able to make a close observation. The act of copulation is similar to that in the case of *C. limosus*, as described by Andrews (1904), but the male does not take hold of the anterior walking feet of the female with its chelæ, and its second pereiopods are clasped around the carapace of the latter, lying in the cervical groove, and almost touching each other on the back of the female. In this case it was the fifth pereiopod of the left side, which was stretched across the sternum in order to elevate the copulatory organs. The male of this couple was 67 mm. long, the female 73 mm. long. The other observation occurred on October 6, 1905, when I found two couples together at Weskit, near Kittanning. The male of the first couple was 63.5 mm., the female 59 mm. long. In the other couple both male and female were 63 mm. long. Both couples separated when captured, and thus I cannot give particulars.

These two dates are so far remote from each other that it seems hardly probable that they belong to one and the same breeding season. It is possible that one of them is exceptional, but I have no means of deciding this. On the other hand, as we shall see presently, spawning takes place at such different times of the year that very likely the mating-season is also irregular.

Females with eggs have been found on the following dates : July 6, 1905; July 10, 1905; July 20, 1904; July 29, 1905; August 1, 1905; August 9, 1904; August 10, 1905. The number of eggs was between seven and one hundred and thirty-three, the smallest number being found in the smallest individual, 59 mm. long. In addition I took a number of females with young under the abdomen. The following records are at hand. At Princeton, New Jersey, in February, 1898. The exact date is not recorded, but it was toward the end of the month. The length of the female was 48 mm., the number of the young was ten.⁸⁰ Further : March 31, 1905;

⁵⁰ This number is unreliable, but represents as many as were secured. In some cases quite a number of the young dropped off when the mother was captured.
length of mother 71 mm., ten young; August 18, 1904, length 59 mm., ninety-two young; September, 20, 1905, two eases, one 53 mm., long, with thirty-nine young, and another 55 mm. long, with thirty-five young; November 8, 1905, 73 mm. long, with one hundred and eleven young; November 22, 1905, two eases, one 84 mm. long, with seventy-five young, and another 67 mm. long, with sixty-eight young.

This extends the spawning season over the following months : February, Mareh, July, August, September to November. Since young were found in February and November, these must have been in the egg-stage at least a month before they were eaptured, and this would add January and Oetober. Thus we have only interruptions in December and from April to June. The gap in December may easily be filled, and be due only to the incompleteness of our investigations in winter, but the gap in April, May, and June may be real.

If there is any spawning-season in *C. bartoni* it would eover nine months of the year, from July to Mareh. This, however, is entirely different from what we have seen in the river species, where the spawning season falls exactly in the months where no spawning has been odserved in *C. bartoni*. And besides, this gap may be partly filled in *C. bartoni*, for I have found very young specimens (between 10 and 20 mm. long; the newly hatched young are 9 to 11 mm. long) on the following dates: May 16, 1905 (13 to 14 mm.); May 25, 1905 (11 mm.); June 2, 1905 (about 17 mm.); June 12, 1905 (14 mm.); June 17, 1905 (15 mm.); August 22, I905 (10 to 11 mm.).

The eonelusion is that very likely *C. bartoni* has no defined spawning-season, but may spawn at any time of the year, and that accordingly the mating-season is also not restricted to a particular part of the year. The latter is further substantiated by the fact that males of the first form are found practically all the year round. I have the following dates: March 21, 28; April 19; May 7, 9, 17, 21, 25, 27, 30; June 2, 3, 6, 12, 13, 16, 23, 24; July 10, 12, 18, 26, 29; August 1, 10, 18, 22, 26; September 11, 16, 20, 21, 30; October 5, 6, 10, 12, 17, 24, 31; November 8, 22; December 25. The only two months missing are January and February, when no collecting was done. On the other hand males of the second form are also abundant all the year round, and were found, with the exception of January and February, in every month.

Under these eireumstanees it is impossible to say anything about the life-eyele of the single individual, since different generations cannot be traced. But one thing should be mentioned. The males of this species do not seem to attain sexual maturity as early as the river-species. The smallest male of the first form ever found in eastern Pennsylvania is 49 mm. long, and in western Pennsylvania 50

mm. long. The smallest female with eggs or young is from New Jersey (Princeton), and is 48 mm. long. From the eastern part of our state I have seen none smaller than 55 mm. long, and in the western part the minimum is 59 mm. in length. This is considerably above the minimum size of sexually mature specimens of C. obscurus and agrees better with C. diogenes.

In one case I have been able to observe the increase in size which takes place upon moulting. On July 11, 1905, I found at Tionesta, Forest County, a female in the act of shedding, and succeeded in keeping her alive till the new shell was hard enough to be measured. The old shell was 32 mm. long, and the new one 36 mm. in length. In this case the crawfish withdrew from the old shell through a crack that appeared on the dorsal side between the carapace and the abdomen.

We have seen above that the regular seasonal cycle observed in the river-species is probably due to the regular and considerable changes of temperature taking place in the rivers. *C. bartoni* lives in small streams, which generally are much cooler in summer than the larger ones, and this apparently explains the difference in the seasonal history. The temperature conditions under which *C. bartoni* is found, are more uniform throughout the year, and consequently no regular seasonal periods in the life are observed.

No previous observations on this species have been published, except Williamson's note (1899, p. 47), that this species was found with young under the abdomen on March 28, 1899, at Columbus, Ohio. This lack of information is rather singular, considering the extreme abundance of this form in the eastern part of the country.

Cambarus bartoni robustus very likely is identical in its life-history with the typical form. I have made observations at only a limited number of dates, but they tend to show that there are no marked seasonal periods.

The following dates for the capture of males of the first form are at hand: May 27, 1904; July 11, 1905; August 22, 1905; September 18, 1900 (Atkinson collection); September 30, 1905; October 4, 1904; October 6, 1904; November 14, 1903 (Mus. Oberlin). The smallest male of the first form measures 63 mm. in length.

Males of the second form were taken in the months of May, June, July, August, September, and October. They were abundant in every case, considering the number of specimens secured.

Copulation was never observed. A female with eggs was found on July 11, 1905, at Spartansburg, Crawford County. It was 84 mm. long, and the number of eggs was 228, more than twice the number of those usually observed in the typical *C. bartoni*. Young specimens, less than 20 mm. long, were taken on May 27, 1904 (18 mm.); and were numerous in a lot collected by Miss G. Kinzer on August 27, 1905 (9 to 16 mm.).

For the months of December, January, February, March, and April, no records are at hand.

6. Cambarus monongalensis and Cambarus carolinus.

The temperature conditions under which these two species are found are similar to those observed in the case of *C. bartoni*, and they are even more uniform, considering the fact that both are exclusively restricted to spring-water, avoiding even small streams. In 1905 I took the following measurements of the temperature of the water in the holes of *C. monongalensis* (May 16 at Morgantown, the rest at Edgewood Park); March 18 (ground still frozen in places); 39° F.; May 16, 58° F.; July 8, 63° F.; August 18, 68° F. The range is considerably less than that given for *C. obscurus* (35° to 80° F., see above, p. 479). We consequently should expect a similar irregularity in the seasonal history as in *C. bartoni*, differing markedly from the third chimney-builder, *C. diogenes*. This is indeed the case.

My observations are rather complete with reference to *C. monongalensis*, covering the time from March 18 to December 26. During no period within this time were males of the second form absent or scarce, but males of the first form were also almost regularly found; the following are the dates for the latter: March 18; April 4, 21, 24; May 1, 6, 9, 16, 21, 24; June 3, 30; July 6, 8, 20, 24; August 7, 13, 18; September 10; October 9, 10; November 8.

Copulation was not observed; but in one case, May 6, 1904, (Fern Hollow), a male of the first form and a female (55 and 72 mm. long respectively) were found together in the same hole. The smallest male of the first form ever found was 53 mm. long.

Females with eggs were obtained on June 25, 1906 (O. T. Cruikshank); June 28, 1905, (three specimens); June 30, 1904, and July 20, 1905. These few observations would tend to restrict the spawning-season to the months of June and July, but this conclusion is not admissible, since newly born young are found at various other parts of the year. I have such (less than 20 mm. long) taken from the hole of the mother, at the following dates: April 4, 1905 (13 mm. long); April 29, 1905 (18 mm. long); May 1, 1905 (17 to 20 mm. long); May 2, 1905 (16 to 21 mm. long); May 6, 1904 (19 mm. long); June 11, 1904 (19 to 20 mm. long); August 18, 1905 (14 mm. long); September 24, 1898 (19 mm. long and above, collected by Rhoads and Williamson); October 29, 1904 (19 mm. long). This extends the spawning-season considerably, but it has the appearance of being interrupted during the winter.

The smallest female with eggs is 58.5 mm. long. The number of eggs is between thirty-eight and seventy-nine, which is considerably less than in the river species, and also on the average slightly less than in *C. bartoni* and *diogenes*.

In this species the young of one litter seem likewise to grow at a different rate. Thirteen young found with the mother in the same hole on May 2, 1905, were between 16 and 21 mm. long. Ten young found on June 16, 1904, were from 20.5 to 32.5 mm. long. Twenty-two young, found on July 20, were from 22 to 27 mm. long. Twenty-four specimens dug out with the mother by Rhoads and Williamson⁸¹ on September 24, 1898, are from 19 to 29.5 mm. long.

Thus it seems that C. monongalensis agrees well with C. bartoni. No well-marked spawning-season is present. At any rate the spawning-season extends over a very large part of the year, and, correspondingly, no well-marked mating-season can be distinguished. Males of the first form may be found at any time, and also males of the second form. Sexual maturity is delayed, males turning into the first form comparatively late, and the females also are not mature before they have reached a larger size than the river species. In all these respects, except sexual maturity, C.monongalensis differs from C. diagenes.

There are further differences from *C. diogenes* in the development of the young. We have seen that young *C. diogenes* remain in the hole of the mother for some time after they have left the abdomen of the latter. When hatched they are about 9 or 10 mm. long, and leave the mother very soon, since free individuals have been found only 10 mm. long. When they have grown to about 20 mm. in length, they leave the hole of the mother.

In C. monongalensis, however, they stay considerably longer in the hole of the mother. The exact time cannot be ascertained, but we can draw conclusions from their size. Free young specimens from 13 to 25 mm. in length are always found with the mother. The smallest specimen which had begun to make a hole of its own was 26 mm. long (August 7, 1905, Fern Hollow). Another was 29 mm. long (October 28, 1905, Edgewood Park). Specimens over 30 mm. long generally have built their own burrows. But there are exceptions. As we have seen, young up to 32.5 mm. long have been found with the mother; and further, on July 24, 1905 (Deer Lick), I took out of one hole fifteen young, measuring from 27 to 33 mm. in length, and out of another hole three young measuring 37, 39.5, and 40 mm. in length. In these cases the mother was also in the hole. Although in the last two cases conditions seem rather abnormal, it is certain that the young of C. monongalensis remain longer in the hole of the mother than those of C. diogenes. While the latter begin to shift for themselves when about 20 mm. long, young specimens of C. monongalensis do not do so before they reach 25 or 30 mm. in length, and may even postpone this step till they have attained a larger size (maximum 40 mm.).

⁸¹ Williamson (1901, p. 12) says that there were forty-seven young ones: only twenty-four are now in the collection of the Carnegie Museum (Cat. No. 74. 25). Possibly this discrepancy is due to a misprint.

I once observed the change of a male from the second form to the first form. The specimen was 58 mm. long, and was dug out of its hole on August 18, 1905, at the type locality, Edgewood Park. It was kept in a jar in water, and had moulted on August 30. I had been away on an excursion on the two preceding days, but on August 27 it had not yet shed. When the fact was discovered it had eaten the larger part of its old shell, only the claws remaining, which were also eaten up subsequently, all but the finger-tips, by September 4. The new shell measured 61 mm. in length. When captured this specimen was of the second form. After moulting it was of the first form.

On account of the irregular spawning season it is impossible to trace the life-history of one and the same individual, and consequently we cannot draw conclusions as to the duration of life.

The few observations on *C. carolinus* entirely agree with those made on *C. monongalensis.*

Males of the second forms were found in May, June, July, August, and September. For males of the first form I have the following dates: May 17, 1905; June 24, 1904; August 2, 1905; August 11, 1904; August 12, 1904; September 5, 1905; September 7, 1904; October 16, 1905. The smallest male of the first form measures 56 mm. in length.

Two females with eggs were secured on July 12, 1904. One was 80 mm. long, and had only three eggs; the other was 77.5 mm. long, and had seven eggs. These numbers seem strangely small, and apparently are not normal, for on August 1, 1905, I found a female 69.5 mm. long, with twenty-two young under the abdomen. But even this number is below the average of *C. monongalensis*. While these cases seem to indicate a spawning season in July, the finding of very young ones in the hole of the mother at other dates considerably extends this period. I have found such on May 17, 1905 (17 to 21 mm. long); June 13, 1905 (14.5 to 21 mm. long); August 1, 1905 (18 to 23 mm. long); August 2, 1905 (28 mm. long); August 9, 1904 (17 to 25 mm. long); August 11, 1904 (19 to 29 mm. long).

The largest young remaining with the mother were 29 mm. long, while the smallest in a hole by itself was 30.5 mm. long. Thus the time of leaving the hole of the mother is about the same as in *C. monongalensis*.

The above observations are not at all sufficient to show that *C. carolinus* agrees entirely with *C. monongalensis*, but since both [species are alike in so many particulars, morphological and ecological, and since the above dates do not show any differences, we may safely assume that the life-history of both species is similar.

The seasonal history is rather well known in four of the species above discussed,

C. obscurus, C. bartoni, C. monongalensis, and C. diogenes. These are the species found in Allegheny County, and they are most complete, since I had the best chance to study them, three of them being found in the immediate vicinity of my residence and the fourth (obscurus) within a few miles and within easy reach.

We are able to distinguish two main types of life-history, which I should like to call for convenience the *warm water* and the *cool water types*. *C. obscurus* and *diogenes* represent the first, and agree with each other in having well marked matingand spawning-seasons, and in early summer a period when no males of the first form are found. They differ, however, in the fact that in *C. obscurus* sexual maturity is reached, as a rule, at the end of the first summer, which does not seem to be the case in *C. diogenes*. Of the other species, of which no complete series of dates are at hand, the river-species, *C. limosus*, *C. propinquus*, and *C. propinquus sanborni*, very likely agree with *C. obscurus*, for the comparison of the dates does not reveal any differences.

The cool water type is represented by C. bartoni and C. monongalensis. Both are characterized by the absence of well marked mating- and spawning-seasons. They may be expected in any stage of development at any part of the year, even winter making no exception. C. carolinus probably belongs also to this type, although the observations are too scanty to positively establish the fact.

One thing in conclusion should be especially emphasized. The life-history and the habits of different species of the genus *Cambarus* are by no means similar. On the contrary they differ considerably, and the differences may be accounted for primarily by the different ecological conditions under which they live. Consequently it is inadmissible to generalize from facts observed in one species only, and further it is to be expected, if other species are studied, that additional types of life-history will be discovered.

VI. ECONOMIC VALUE.

1. Popular knowledge of Crawfishes.

The crawfishes of this state are generally well known to the population. They are abundant and large enough to attract the attention even of the casual observer. But it is chiefly the small boy who is interested in them. Three popular names are employed for them, *crab*, *crayfish*, and *crawfish*. "Crab" obviously is a misnomer, belonging originally to the marine *Brachyura*, but it is largely in use all over the state, and chiefly so in the cities. The word "crayfish" is used the least. In my experience I heard it mostly in the mouths of such people as had a certain amount of schooling and had acquired some knowledge of natural history. This word is

preferred by teachers generally, very likely in consequence of its use in one of the standard works on these creatures (Huxley, "The Crayfish"). The third word, "crawfish," is the proper American name. I found it commonly in use in the rural communities where "crayfish" and "crab" were often entirely unknown. This is chiefly the case in the southwestern section of the state and in West Virginia. In one or two cases in Fayette and Somerset Counties I heard a distinction made between "crab" and "crawfish." The former name was used for the river and brook forms, *C. obscurus* and *C. bartoni*, the other for the chimney-builders. All three words go back to the same root, Old German *krebis*, from which is derived on the one hand the modern German *Krebs*, and the English *crab*; on the other hand the French écrevisse, the English *crayfish*, and the American *crawfish*. The latter form, being typically American, and being exclusively known to the natives of a large part of the country (the farmers), I have decided to use it in preference to the other two forms.

In literature "crawfish" was used by Say (1817), Harlan (1835), Hagen (1870), Abbott (1873), Hay (1896). "Crayfish" was used by Abbott (1884 and 1885), Faxon (1885, 1890, 1898), Hay (1893, 1899), Andrews (1895, 1904), Shufeldt (1896), Osburn and Williamson (1898), Harris (1900), Williamson (1901, 1905). Thus "crawfish" has the priority.

Other names have been given incidentally. Rafinesque (1817) calls *C. limosus* "mud lobster," (I heard this name once in Delaware County). Say (1817) and Harlan (1835) call *C. bartoni* "freshwater lobster," and Williamson (1899) uses the abbreviation "cray."

2. The use of crawfishes as food and bait.

Although well known, crawfishes are not much used as food by the population of Pennsylvania; but this is generally the case in the United States. In some of the larger cities of the United States they are found more or less regularly on the market (see Ortmann, 1900, p. 1260), *C. limosus* being one of the species which is principally used for food. I have, however, never heard that this is the case in our own state, but it may be found in the markets of Philadelphia.⁸²

Nevertheless crawfishes arc eaten in this state, but not regularly. I have heard sometimes from boys that they had tried them, but only in "sport," and only exceptionally have I met persons who had eaten them repeatedly and were fond of them. Generally, this source of food is unknown to the masses in this state. Yet a dish of crawfishes is not to be despised. It is true, our species never attain the size of the

⁸²Rafinesque (1817, p. 42) says of C. limosus at Philadelphia, that it is "good to eat."

highly esteemed European forms, but I know from my own experience that, as regards quality, the former are not inferior to the latter. Young specimens (and chiefly soft shells) may be fried in butter and eaten shell and all, while the abdominal muscles of older ones, when boiled in water, are very good.

Of course, it is hard to create a taste for crawfishes among the masses, but I do believe that it would be worth while to try. Crawfishes are so abundant in certain parts of the larger rivers, *C. limosus* in the Delaware, and *C. obscurus* in the Ohio drainage, that it is easy to get any amount of them. It also would not be difficult to raise them, for instance in ponds, and to supply the market regularly and judiciously. And further, I do not see, why the "tails" (abdomen) could not be used for canning, exactly like the tails of shrimps and prawns.

Beyond this, crawfishes are used only as bait by fishermen. This use is quite general, and crawfishes form an important part of the fisherman's outfit especially in western Pennsylvania. They are most valuable in fishing for Black Bass (*Micropterus*), since these fishes seem to be very partial to this bait.

3. Crawfishes as scavengers. Their food. Their enemies.

The indirect economic value of crawfishes is best expressed by saying that they are scavengers, as decapod crustaceans in general. They dispose effectively and quickly of any decayed matter, animal or vegetable, coming within their reach. They also eat living creatures. This was known previously. Abbott (1873, p. 83) calls them (C. limosus and bartoni) "omnivorous," and "scavengers," and says that they eat water-weeds, and seize young Cyprinoid fishes. Andrews (1904, p. 175) fed C. limosus in the laboratory on raw and cooked meat, raw eggs, pieces of earthworms, and on Chara and Hydrodictyon. Williamson (1901, p. 12) reports that C. monongalensis was caught in traps baited with raisin and oatmeal. I used for my specimens in the laboratory all kinds of meat, and since I am especially fond of smoked sausage, I let them often partake of it when I had it for lunch. They also eat earthworms and green vegetable matter, for instance seedlings of several weeds (Galinsoga, and Rumex acetosella), grass, and water-weeds (Vallisneria). In nature they are often found at carcasses and other animal refuse lying in the water. They eat insects. For instance I have seen C. bartoni taking grasshoppers used as bait while fishing for trout (Tub Mill Run, Ross Furnace, Westmoreland County). In the case of the chimney-builders vegetable matter seems to be largely resorted to, not only fresh plants, but also decaying vegetation being used. In digging them out of their holes I repeatedly found masses of decaying leaves and the like lodged in some side branch of the hole in such a position that they could not have fallen in acci-

dentally, but must have been brought in by the crawfish. In one case (October 9, 1905, Nine-Mile Run), I found in a side-pocket of a hole of a female *C. monongalensis* a number of ripe fruits of *Cratægus*, about a handful, which under no circumstances could have fallen into the position where they were found. The hole was under a large *Cratægus* bush.

Thus it seems that any vegetable or animal matter, either fresh, or decaying, serves as food for crawfishes, and although some species may prefer certain classes of food on account of taste or necessity, they all take readily to any kind, as is seen by the fact that in captivity they eat everything that is offered to them without discrimination. If nothing is given, they eat one another.

Crawfishes in turn serve as food for many animals, chiefly those which are aquatic. Among mammals we know that raccoons hunt for them. As has been mentioned above, birds eat them, and the kingfisher and other equatic birds do so quite regularly. The report of Audubon, (see Ortman, 1900, p. 1250), that the White Ibis captures the chimney-builders by throwing fragments of the chimney into the hole, and watching for the crawfish to come up, does not seem strange to me. At Ohiopyle I was told that a domesticated turkey kept upon the grounds of the hotel had the habit of watching the holes of *C. carolinus*, and that frequently he captured this species. I have myself seen this turkey standing motionless before a hole, but I did not observe the actual capture. I do not entertain the slightest doubt that this and other birds are able to catch crawfishes in this way, and do not think that it is necessary to drop dirt into the hole, since the crawfish comes up frequently on its own account, when it may be seized.

Crawfishes constitute an important part of the diet of certain snakes, more particularly of the water-snakes, *Natrix sipedon* and *leberis*. I have seen the latter disgorge *C. obscurus* when captured. (See also Atkinson, Ann. Carn. Mus., I. 1901, p. 149, 150.) On two occasions I have found garter snakes, *Eutænia sirtalis*, in holes of *C. monongalensis*; two specimens of this snake in one hole on October 18, 1904, (Fern Hollow), and one snake in a hole on October 28, 1905, (Edgewood Park). However, whether the snakes were after the crawfishes, or whether they simply were using the holes for winter quarters, remains doubtful.

Professor H. A. Surface writes to me that *Cryptobranchus allegheniensis* and *Necturus maculosus* are among the chief enemies of the crawfishes, and, indeed, these two salamanders are generally found at places where crawfishes abound. (Compare Eydeshymer, American Naturalist, XL, 1906, p. 128.)

They are, however, most valuable as food for the fish-fauna of our waters. As has been mentioned above, crawfishes are good bait for certain fishes, and it is very

likely that many of our freshwater fishes depend largely upon crawfishes for nutriment. It would be interesting to investigate how far this mutual correlation between fishes and crawfishes holds good in our state. The presence of a riverspecies in our western streams, and its absence in any drainage systems in the central parts is very remarkable. Indeed *C. bartoni* is found in rivers, but only occasionally, and in small numbers. My own observations are not sufficient to give an approximate idea as to these relations, since I did not pay much attention to the fish-fauna, and the latter has decidedly deteriorated, at least in quantity, and the fish have become rather scarce in most of our streams. Possibly the decrease in the number of fishes has caused an increase in the number of crawfishes.

4. Crawfishes as obnoxious creatures.

For the river-species hardly a point can be mentioned which would tend to show that they are obnoxious to human interests, except the fact that they occasionally capture young fishes. It is different with the burrowing species; which often become troublesome. In regions where chimney-builders are abundant I have repeatedly heard complaints about the chimneys, and chiefly so in the case of *C. carolinus* in Somerset County, Pennsylvania, Garrett County, Maryland, and Preston County, West Virginia. Here the mud-piles may hamper farming operations by interfering with the harvesting machines, clogging and ruining them. At Selbysport, Maryland, I was told that conditions were so bad that the farmers tried to exterminate the crawfishes by throwing unslacked lime broadcast over the fields, which operation was partly successful, the crawfishes coming out of their holes by hundreds in a dying condition. I was told that this treatment, repeated several times, had considerably reduced the numbers of the red crawfish in this neighborhood. At no other place did I hear of attempts made to kill these crawfishes, although farmers were unanimous in denouncing them as a nuisance.

At a few places another complaint was made, namely, that the chimney-builders were cutting off and eating up sprouting crops. This was affirmed with reference to *C. carolinus* at Reedsville, Preston County, West Virginia, where a farmer told me that this species had cut off the largest part of a crop of buckwheat, so that practically nothing was harvested. At Parson, Tucker County, West Virginia, complaints were made that the same species had damaged sprouting corn; and at New Martinsville, Wetzel County, West Virginia, I heard that *C. diogenes* was charged with eating up all kinds of sprouting crops, corn and beans being especially named.

I do not doubt that these complaints are justified, and that the burrowing species

actually eat and damage crops to a considerable degree. As I have observed, in captivity *C. monongalensis* and *C. diogenes* eat young plants, and they surely do so when not in captivity, young sprouting corn, buckwheat, etc., being rather succulent and attractive to them. If sown in a place where crawfishes abound these crops will surely be attacked.

This being the case, and besides the chimneys being also a nuisance, it might be desirable to exterminate the crawfishes in a given locality, or at any rate to reduce their numbers. For this purpose unslacked lime, the means employed by the farmers at Selbysport, might be used. But I am in no position to vouch for the efficiency of this remedy, having no personal experience (with the exception of the one case mentioned above, p. 346). I simply report what was told me.

Another way might be to drain the places where crawfishes are plentiful. But this hardly will be as efficient a means as desired. Drainage only lowers the level of the groundwater, and in the case of *C. carolinus*, which is the chief offender, we know that it digs down sometimes over three feet to reach the groundwater. In Rainier Park at Ohiopyle this species used to be very abundant, but the draining of the park has reduced its numbers. Still it is present there, and the chimneys are thrown up all over the lawn, where the holes must in places go down at least three feet before reaching water. Thus, although a decrease in numbers may be brought about by drainage, a complete extermination by this method must not be expected.

Another form of damage done by chimney-builders is known. They are reported to burrow into and to do damage to the dams on ponds, reservoirs, and rivers. (The levees of the Mississippi. See Ortmann, 1900, p. 1262.) No instances of this kind are known to me in Pennsylvania. In one case, at the reservoir of McGee Run, at Derry, Westmoreland County, I saw holes of *C. diogenes* not only along the banks, but also in the dam. The specimens were all young, and the holes small, since this reservoir has existed only for a few years. But it would not be astonishing if the crawfishes should gradually work deeper into the dam, finally causing serious damage.

VII. BEARING OF THE ABOVE STUDIES ON THE THEORY OF EVOLUTION.

Our observations on the Pennsylvania crawfishes, morphological, ecological, and geographical, serve to illustrate certain phases of the process of evolution, and certain theories propounded in connection with them. Naturally they do not elucidate this process in its fullest scope. Thus I shall only pick out a few points upon which my observations may have some bearing.

1. The Mutation Theory of De Vries.

The latest fashion in evolution theories is the so-called "mutation theory" of De Vries (De Vries, 1905). It is much discussed at present, and the general trend of opinion is that, although De Vries' idea of the origin of species may not hold good in all cases, he certainly has demonstrated at least one way by which species may be formed. It is generally maintained with emphasis that his experiments are beyond doubt and that the facts demonstrated by him cannot be denied.

This indeed is the case, and it would be lamentable if any of the statements presented by De Vries as facts should prove to be unreliable. I am decidedly of the opinion that the statements are correct, but I also hold that De Vries was not the first to bring the facts forward. They belong to a class that was known long ago. But furthermore, I believe that the conclusions drawn by De Vries from these facts are entirely wrong.

I recently have devoted several articles to demonstrate this, and shall not again go into detail here (see *Science*, May 11, August 17, and November 30, 1906).

However, I shall discuss here a special part of De Vries' theory, which concerns the distinction he makes between "fluctuating variation" and "mutation." The latter is said to be characterized by "sudden leaps," while the former is said to be by "small steps." Although De Vries sometimes does not lay much stress upon this distinction (see Copeland, 1904, p. 421), this difference is often regarded as paramount in his theory (see MacDougal, in *Popular Science Monthly*, vol. 39, 1906, p. 207). And since De Vries believes that species are formed only by mutation, it should be expected that the morphological differences between existing species should at least frequently exhibit signs of "sudden leaps." If such leaps are observed in our species of *Cambarus*, this would tend to support this part of De Vries' theory; if not, the theory that mutations are always or generally marked by discontinuity of variation, should be dropped.

2. Species, Varieties, and Variations among the Pennsylvania Crawfishes.

I have distinguished in the systematic part of this monograph seven species and one variety among the Pennsylvania crawfishes. Besides I have discussed another extralimital variety. This means that the characters distinguishing these forms are different in their taxonomic value, and the reasons for thus estimating them should be given.

The seven species of Pennsylvania belong to two subgenera, *Faxonius* and *Bartonius*, which are distinguished by very sharp differences in the male copulatory organs.

The subgenus *Faxonius* is represented in our state by three species : *C. limosus*, *C. propinquus*, and *C. obscurus*. The first is geographically, as well as morphologically, separated from the other two; and here again it is the shape of the male organs which serves as the chief distinguishing feature. Besides there are other characters, such as the shape and the spinosity of the carapace, which make it possible to recognize *C. limosus* at a glance. No transitional forms being present, the standing of *C. limosus* as a "good species" is beyond doubt.

It is different with C. propinguus and obscurus, and the extrahimital form C. sanborni. These three resemble each other very closely, and it is hard, indeed impossible, without close examination to distinguish them. They also live under similar ecological conditions, and their ranges together form a unit, so that it is evident that they are closely allied genetically. The differences of C. obscurus from the other two forms are furnished by the "shoulder" of the male organ and the tubercles of the annulus of the female, together with the complete lack of the median keel of the rostrum. Other differences, such as sculpture and spinosity of the chelipeds, are of secondary value and not entirely reliable. But it must be emphasized that within the established range of C. obscurus, from Fish Creek in the southern part of the Panhandle of West Virginia to the upper Alleghany and the Genessee Rivers in McKean and Potter counties, and from Cheat River at the West Virginia stateline, to the upper Shenango River in Crawford County this species is remarkably uniform in the characters mentioned. No specimens have been found within this area which show the slightest tendency toward C. propinguus.

Thus, with reference to this form, the postulate that a species should be sharply and constantly separated from the coexisting allied forms is fulfilled (see Ortmann, 1896, p. 191) and accordingly I regard *C. obscurus* as a good species.

As regards *C. sanborni*, matters seem to be slightly different. It agrees in the shape of the sexual organs with *C. propinquus*, and differs only from the latter in the lack of a rostral keel and some minor features in the armature of the chelipeds. In the lack of a rostral keel it approaches *C. obscurus*, but always may be distinguished by the shape of the sexual organs. Its relation to *C. propinquus* remains doubtful. My observations do not cover the region in which possible transitions might be expected (northern and western Ohio), and thus I must leave this question open, and I follow Faxon in regarding *C. sanborni* as a variety of *C. propinquus*. But it should be possible to settle this question by proper investigation, and I would not be astonished if it should be finally discovered that *C. sanborni* actually is a good species, sharply and constantly separated from *C. propinquus*.

The subgenus Bartonius contains four species in Pennsylvania. One of them,

C. bartoni, differs from the rest ecologically as well as morphologically. It is distinguished by a number of characters, and there is no possibility of morphologically intermediate forms, so that *C. bartoni* not only is a good species, but also belongs to a different section of the subgenus.

C. bartoni possesses in Pennsylvania a variety, C. bartoni robustus, which, according to my experience, is constant, and never runs into the typical form. It also seems to occupy a slightly different territory, although often found associated with the latter. These facts would justify us in regarding it as a good species. I have not done so in the systematic part, since the facts at hand are too meagre to finally decide this question. The range of C. robustus in Pennsylvania is only a small part of the area occupied by this form, and in the states of Ohio, New York, and in Canada, the conditions are entirely unknown. Furthermore a form similar to our robustus, although, as it seems to me, not entirely agreeing with it, has been reported from Virginia, Maryland, and Kentucky, and before particulars about the relation of this form to C. bartoni and to our robustus are known, we cannot judge as to the taxonomic position of C. robustus. Therefore I have refrained from modifying the position hitherto assumed, that this form is a variety of C. bartoni.

The other species of the subgenus *Bartonius* in Pennsylvania are *C. carolinus*, *C. monongalensis*, and *C. diogenes*. They belong to the *diogenes*-section, and all three are closely allied. *C. carolinus* and *monongalensis* are more nearly related to one another than to *C. diogenes*. The latter apparently is a more advanced form.

C. carolinus and C. monongalensis are distinguished by rather insignificant morphological characters, discovered in the shape of the rostrum and the armature of the chelipeds. But the difference in color is so striking that it is impossible to confound them in the field. Other characters also, although slight, hold good according to my experience, and I never have seen intermediate specimens. Moreover the distribution of these two forms is very characteristic, they being sharply separated topographically, and never being found associated at the same locality. Thus all requirements leading us to pronounce them good species are met. Of course this applies only to conditions in Pennsylvania, Maryland, and northern West Virginia; whether they are the same or different farther south remains to be seen.

C. diogenes is more sharply separated from the species just discussed, and there is no possibility of mistaking this species, more particularly as the color is markedly different. But the morphological characters are also very nicely expressed, so that in a case of a red (albinistic) specimen of this species I was not a moment in doubt that I had to deal with *C. diogenes*, and not with *C. carolinus*, although the latter was found associated with this form at this particular locality (Dunbar). There is

no doubt that *C. diogenes* is a good species, and even when discovered in company with *C. monongalensis* or *C. carolinus* we found no intermediate forms which might render the identification uncertain.

As has been demonstrated above, there are two races of C. diogenes in Pennsylvania, an eastern and a western. They never have been distinguished before, and indeed are very similar, so that it is hard to tell them apart. But I think I am able to do so. The differences are very slight, but I never observed intermediate forms, and their existence is improbable, the ranges of the two raees being widely distant from each other. The constancy of the differential characters being the only eriterion of specific difference, while the amount of difference is of no consequence at all,⁸³ we might regard the eastern form as a different species from the western. This may prove to be the correct view, and then the eastern form should be ealled C. diogenes Girard, and the western possibly C. obesus Hagen. I have not taken this course in the systematic part, since our knowledge of C. diogenes is by no means complete. I know only the conditions in this state, but the eastern range of this species extends over large parts of the coastal plain, while the western occupies a vast territory reaching to the Rocky Mountains and the Gulf. It is also not impossible (although improbable) that the eastern and western areas are connected somewhere, (in Virginia?). Before this question is finally settled, and before we know more about the conditions under which C. diogenes occurs in the extralimital parts, it is best to refrain from expressing a positive opinion. Nevertheless it is quite possible that there is a tendency in C. diogenes to split into varieties and species. A variety has been distinguished in Louisiana.

We see that in certain forms my studies have led to a positive decision as to their taxonomic position. In other cases my observations must be completed and supplemented by additional evidence to be gathered in other parts of this country before a final opinion can be reached. The fault is not with the material at hand, but with the insufficiency of our knowledge of the extralimital parts.

As to *variations*, that is to say, occasional aberrations from the typical form, we have seen that such are extremely rare among the Pennsylvania crawfishes, and have in most cases the character of freaks. Some of them, however, are interesting from eertain points of view.

No variations were discovered among one hundred and nineteen individuals of *C. limosus.* With reference to *C. propinquus* in Erie and Crawford Counties, I have pointed out that there is a certain amount of variation in the development of the

⁸³ De Vries (1905, p. 127) talks of "an old rule in systematic botany, that no form is to be constituted a species upon the basis of a single character." This rule is entirely unknown to me in botany as well as in zoölogy.

keel of the rostrum, and in that of the spines and the carpopodite and meropodite of the chelipeds, and we have also seen that there is sometimes a notch on the anterior margin of the male organ. All these characters mark a certain inclination toward *C. obscurus* which will be discussed below.

The six hundred and eighty-seven specimens of *C. obscurus* at hand are, as has been seen above, very uniform in their characters. A tendency has been observed toward an increase of the spines of the meropodite of the cheliped in a direction from the northeast toward the southwest within the range of this species. Here we have apparently the first step toward the formation of a variety: a variation becomes more frequent in the southwestern part of the range, possibly in consequence of hereditary transmission, and begins to "breed true." But it is only the beginning of it, the varying form not being found to the exclusion of the original, and thus it remains "variation" only.

Other variations (mentioned p. 375 and 376) are very likely due to injuries received during life⁸⁴, and again others are of the character of freaks, namely the two cases of apparent hermaphroditism. One of these is rather interesting (Pl. XXXIX, Fig. 7^d and 7^e). Here the male sexual organs do not at all correspond to the typical form of this species, but approach in shape to that known in the *limosus*-section. It seems to me that we have to deal here with a case of atavism. The *limosus*-section has been regarded as the most primitive type of the subgenus *Faxonius*, on account of the very slightly separated tips of the copulatory organs. The *propinquus*-section is next to it, but here the tips are separated for a greater distance. It is quite probable that the latter section descended directly from the former, and it seems that in the instance discussed the sexual organs have reverted to the original *limosus*-type, and thus the assumption that the *propinquus*-section is a descendant of the *limosus*section gains additional strength.

In the seven hundred and twenty-five specimens of *C. bartoni* we again have to emphasize the great uniformity of the characters. The variations discussed are rather insignificant, and consist chiefly in the shape of the rostrum and the size. A single individual has been observed in which one lateral spine of the carapace was present, apparently an atavistic feature. Other variations are of the hermaphroditic type.

No remarkable variations have been found in C. carolinus, and a few insignifi-

⁸⁴ Variations due to injuries are most frequently observed in the case of regeneration of the chelipeds. I did not mention them in the systematic part, since they are very common. If the claws are lost they are replaced by new claws, which differ from the old ones not only in size, but also in shape. The fingers are proportionally longer, and the palm proportionally shorter than in normal claws. This difference in shape remains even if the claws, after repeated monlts, again attain a good size. Regenerated claws may always he recognized by the short palm and long fingers.

cant ones in *C. monongalensis.* The same is true of *C. diogenes*, leaving out of account the differences between the eastern and western forms. The most important variation is that of the width of the areola. In this there is a tendency toward regional restriction, but it is not complete. The wide areola, being a more primitive character, does not represent the variation, but the original condition, which is retained only in a small part of the range and is even there not general. It is a character that has a tendency to disappear and may be classed under atavism. A case of *albinism* has been observed in *C. diogenes*.

The conclusions from the above observations are that in the *Cambarus* forms of Pennsylvania the morphological characters are very constant, and that the variations observed are generally only slight, diverging very little from the typical conditions. Anything that looks like a "mutation" in De Vries' sense is entirely unknown, for the cases of hermaphroditism cannot be regarded as such, and the cases of atavism and albinism do not fall under it, being clearly of a "retrograde" character (De Vries, 1905, p. 121 et seq.).

Further, even between most of our well established species differences are so slight that they cannot be regarded as representing "mutations," that is to say, sudden leaps in a progressive direction (De Vries, l. c., p. 141). This is most evident in the *propinquus*-section, where the three forms, two of which at least must be regarded as species, are distinguished by such insignificant characters that it is impossible to talk of "leaps" or of "sudden changes." The same is true of the differences, although well marked, being very small, and the "gaps" between these species being infinitesimal. The only striking difference is in color, but before we know what causes the appearance of various colors we cannot express any judgment on this point.

Even in those species which are more isolated from the rest, the differences do not amount to much. In *C. bartoni* the depression of the carapace and the width of the areola differ only in the degree of the development from the same characters in the burrowing species. *C. limosus* is the most strongly marked species, but should not be compared with the other river-species of Pennsylvania, but with its nearest relations in southern Indiana (*C. indianensis* Hay), but then again the difference is small and consists only of quantitative changes in the same features.

Thus the assumption of De Vries, that species have originated by sudden leaps, does not find any support whatever in the conditions seen among the crawfishes of Pennsylvania. On the contrary the close affinity of most of them, and the comparative insignificance of the specific characters, supports the view

that these species have originated out of rather slight variations from the original forms. If this is evident in so small a territory, further investigations only can emphasize this, for additional material can only bring these forms closer together. (See Merriam, 1906, p. 257.)

3. Formation of Species by Isolation, as Exemplified by the Pennsylvania Crawfishes

I have repeatedly maintained that the whole process of evolution in nature which ends in the formation of "species," and which, consequently, may be called "origin of species," is not subject to one single factor alone, such as "natural selection" or "isolation" or "mutation" but that it is absolutely necessary that several factors work together. (See Ortmann, 1896, p. 188 *et seq.*) Indeed none of these factors is new, and they have been discussed by various writers, but generally too much value has been attributed to one or the other of them to the detriment of the rest. I have insisted, on the contrary, that four factors are equally necessary to form species, namely: 1, variation; 2, inheritance; 3, natural selection; 4, separation (l. c., p. 190).

Of these the last one, Separation or Isolation, is the one which forms species. To this is due the fact that the whole mass of organic beings to-day is divided up into a large number of units, which we call "species." If it had never existed or acted the process of evolution would have gone on nevertheless, but the organic world would not consist of species; but since separation always has acted, species are present. This does not imply that species should be everywhere well-marked. This process is going on all the time, and in many cases it is not yet finished, and thus it may be difficult sometimes to say whether a particular form is to be regarded as a species or not; but, as a rule, our inability to declare positively that a certain form is a species is only due to the insufficiency of our knowledge.

Separation (or isolation) should not only be conceived of in its broad topographical and climatic aspect, but is, as I have always maintained, largely also ecological. (See "bionomic separation," l. c., p. 190.)⁸⁵ That it may occur under several forms is amply demonstrated by the Pennsylvania crawfishes, and some form or other of isolation is evident in every case *without exception*. Both topographical and ecological separation are recognizable in our material, while climatic separation is not observed on account of the insignificant differences of climate in the region investigated.

⁸⁵ "Barriers" are not necessary. Merriam, 1906, p. 248, 'thinks that the existence of sharp barriers is necessary for isolation; where such are absent he prefers to use the term "divarication." Possibly the term "habitudinal segregation," introduced by Gulick, 1905, p. 49, and 53 *et seq.* would be appropriate.

(a) C. limosus.

It has been repeatedly emphasized above, as well as in a previous paper, that this species is well isolated morphologically and geographically. I have introduced it as one of the examples for the rule that "morphologically isolated species occupy isolated stations" (Ortman, 1905b, p. 127), and also for the rule that "discontinuity of distribution is a proof of antiquity " (ibid.). Both rules are beautifully illustrated by this species, particularly in contrast to the other rule that "closely alliedspecies occupy neighboring areas." Thus not only the effect of isolation, as producing species, is evident in C. limosus, but it is also seen that the degree of isolation is in direct proportion to the sharpness of the expression of the specific characters. C. limosus is geographically the most sharply isolated species of our crawfishes, its area being several hundred miles distant from that of the most closely allied forms in Indiana and Kentucky. Correspondingly it is also morphologically well marked, being sharply distinguished from the other Pennsylvanian species, as well as from species in the west which arc closely related to it. Isolation in this case is purely topographical, since the ecological habits of C. indianensis seem to be similar, (Hay, 1896, p. 495); though another allied form, C. sloani, differs slightly ecologically, (Faxon, 1885, p. 90).

(b) C. propinquus, C. propinquus sanborni, C. obscurus.

These three forms, as far as our present knowledge goes, are sharply separated topographically, while they agree with each other ecologically, but the topographical boundaries between them are not everywhere uniformly sharp. In fact, the ranges of these three forms are connected on the one side by the Ohio River, on the other side by the basin of the Great Lakes.

As we have seen above, the present connection of these forms is a secondary feature developed during the latter part of the Glacial Period, while anterior to this, at the beginning of the Glacial epoch, different conditions prevailed, which were different in turn from those of still earlier times. The history of these forms was probably as follows. At the end of the Tertiary a form corresponding to these three crawfishes existed in the drainage of the Erigan River. Probably there was only a single species resembling the present *C. propinquus*. This species lived in the Erigan River, as well as in its southern tributaries, and there was no chance for it to split up into different species, although variations may have occurred. When the advancing ice of the Glacial Period covered the Erigan River and thus separated the southern tributaries from each other, the latter formed lakes, and later, by overflow (or other means) they were connected again. Thus the present Ohio was created. The temporary isolation of these rivers at the beginning of the Glacial

epoch had its effect upon the crawfishes living in them. They developed into as many species as there were rivers (three). Probably there was already in Tertiary times a tendency within the Erigan drainage to form variations and even geographical varieties, but the fact that these forms (at least two of them) assumed the character of species is due to the physiographical features of the *earlier Glacial Period*.

After the Ohio was formed, and the connection between the areas of these species was reestablished, there must have been a tendency among them to mix along the course of the Ohio River. How it was in the case of C. propinguus and C. sanborni we do not know. But I have investigated the facts in the case of C. sanborni and C. obscurus. Where they come together in the neighborhood of New Martinsville, West Virginia, C. sanborni shows no tendency at all to go up the river, no trace of it being found above New Martinsville. This apparently is due to the greater difficulty of ascending the river and to contend with a species which is firmly established there. On the other hand C. obscurus apparently has gone down the river, and has invaded the original territory of C. sanborni, but it has done so only to a small extent. For, although it is easier to descend a river, the fact that the region invaded is occupied by another species with the same ecological habits must make it rather difficult to oust the latter. Thus, although C. obscurus has the advantage over C. sanborni, being favored in its migration by the fact that it is here downstream, this advantage is only a slight one, and did not enable C. obscurus to occupy any of the territory of C. sanborni to the exclusion of the latter. It is found here associated with it, but its numbers are small, and the original form still prevails.

A curious fact, however, has been observed. I have pointed out (p. 367 and p. 434) that the specimens of *C. sanborni* captured in Fishing Creek at New Martinsville showed in certain characters an inclination toward *C. obscurus*. This suggests hybridization. Of course it is impossible to ascertain this positively without experiments, but it seems that a crossing between these two forms is not altogether impossible, for the shape of the sexual organs is very similar in both. They are generally very closely allied, and further, their breeding seasons are identical, so that kyesamechania ⁸⁶ probably does not exist. This is further suggested by the conditions observed in the Lake Erie drainage in Pennsylvania. Here *C. propinquus* and *C. obscurus* come together, and again we pointed out (p. 365) that *C. propinquus* in this region has a tendency towards *C. obscurus*. In both cases hybridization would easily explain matters.

²⁶ Impossibility of crossing, due to any cause, mechanical, physiological, or ecological, see Eimer, 1895, p. 14. Gulick (1905, p. 95) calls this "Impregnational Isolation." Under this head falls also Romanes' "physiological isolation."

Even if it should be the case that *C. obscurus* may cross with *C. propinquus* and *C. propinquus sanborni*, this does not invalidate its standing as a species, for we have numerous examples in nature in which true species form hybrids.

Thus we see that these three species, the origin of which as species belongs to the beginning of the Glacial time, have come together again; but each seems to remain in its original area, and where they come into actual contact the one species is hardly able to oust the other. To a small degree hybridization seems to be possible at the points of contact. The assumption that *C. sanborni* might be a hybrid between *C. propinquus* and *C. obscurus* is rendered impossible by the exclusive presence of *C. sanborni* all over its range (excepting Fishing Creek), without any trace of the two other species.

It remains to consider the question what the relation of the specific characters to isolation may be. We see that in the case of C. obscurus it is chiefly the "shoulder" of the male sexual organ which distinguishes this species. This shoulder is found at a place where an external stimulus acts upon this organ, namely, just where it is touched by the fifth pereiopod in the act of copulation. A similar shoulder is found in many other species of *Cambarus* of different groups and even subgenera, and thus it is highly probable that it is this external stimulus which induces the development of this feature. But this does not afford us an explanation why this shoulder did not develop in other species, especially in C. propinquus. At present I am unable to answer this question. The fact remains that we have to deal with a specific character, which is clearly due to an external stimulus,⁸⁷ and I have always held the opinion that every variation is invariably caused by a reaction of the organism to some external influence. (See Ortmann, 1896, p. 188, and 1898, p. 157.) But the view that acquired characters are transmissible is not fashionable, although now admitted by its chief adversary, Weismann. In consequence of the modern tendency to deny the effect of external causes upon variation, at any rate to deny the possibility of the hereditary transmission of such variations, not much attention has been paid to the mutual relations between external stimuli and the reaction of the organism upon them. But here I think much room for investigation is left. In the present case the reaction of the organism upon the external stimulus caused by the contact of the fifth pereiopod with the sexual organ is to form at the point of contact a notch or angle (shoulder) on the sexual organ.

This reaction may be slightly advantageous, but it is not absolutely necessary, for we see that there are many other species in which this reaction has not taken place, even among the most closely allied forms, which are nevertheless well off and

⁸⁷ Under " pressure of the environment," as Merriam puts it (1906, p. 244).

flourishing. In other words, the "selectional value" of this character is practically at the zero-mark. This demonstrates again that the conception of "natural selection" as "selection of the fittest" is incorrect. With regard to fitness there are many characters which are entirely indifferent, and this is one of them. The absence or presence of a rostral keel, and of tubercles in the case of the female annulus, the other specific differences of these forms, belong to the same class. We thus see that natural selection has played no part in the development of these characters of these species. But this does not imply that selection has had nothing to do with the evolution of these species, on the contrary this factor has always acted, and if these characters had not been fit to survive, the species would not have been able to survive. Natural selection (in the modified sense, according to Pfeffer, see Ortmann, 1896, p. 176), resulted in the fact that the *propinquus*-group, such as it actually is, is able to live and to flourish, but it is not responsible for the splitting up of this group into two or three species.

The latter fact is entirely due to *isolation*. In the present case the isolation was in effect only during a short period in the past, but it was enough to differentiate several species. At the present time there is a tendency to undo this effect. These species are beginning to mingle again. But this process has not yet progressed far, and for several reasons will very likely be slow in future. It is hard to say what the outcome will be, whether we shall have a hybrid form, or whether one will suppress the others. *C. obscurus* is the most advanced form, and also seems to be slightly more vigorous than the others. Thus it may finally overrun them and crowd them out, unless it is in turn conquered by a still more vigorous from, *C. rusticus*, advancing from the southwest.

From the above discussion we see that whatever may have been the processes of variation and of natural selection, or independently of what we may think of the possibility of the inheritance of acquired characters, the fact that the *propinquus*-group has split up into species is solely due to isolation, which in this case is strictly topographical. We have here three forms with identical ecological habits, in which topographical isolation is evident, illustrating the rule that "closely allied species occupy neighboring areas." (See Ortmann, 1905b, p. 127, Jordan, Science, Nov. 3, 1905, p. 546, and Merriam, 1906, p. 248, *et seq.*)

(c) C. bartoni.

This species is morphologically well isolated from the other Pennsylvanian species, and also has peculiar ecological habits. Being found all over the state it necessarily comes into contact with all the other species and is often found associated

with them. This is preciminently the case with the river forms, C. limosus, C. obscurus, and C. propinguus.

Here we have an instance in which at a given locality two species may be found side by side. This, however, is due to secondary processes. Originally each of the two species had a different center of radiation, and thus we again see the action of isolation. The center of *C. bartoni* lies in the mountains of the Appalachian system; the common center of *C. limosus* and the *propinquus*-group is in the central basin of the Mississippi, and the special center of *C. limosus* in the coastal plain, and that of the *propinquus*-group in the Erigan and Lower Ohio drainage.

Nevertheless these species came together (see Ortmann, 1896, p. 186), but the migration was in different directions, the river species coming up the rivers, while *C. bartoni* migrated down stream. Although living side by side there is no danger of hybridisation, since their morphological differences are such that kyesamechania exists. The different shape of the sexual organs of *C. bartoni* from that in the subgenus *Faxonius* precludes any idea of their being able to cross. Such cases do not offer anything remarkable, since the occupation of and the association at the same locality of different forms coming from different directions, and not being closely allied, is the general rule in any ecological community (*biocenosis*).

Conditions are slightly different in the cases where *C. bartoni* is found in close proximity to the chimney-builders. Here there is closer affinity, but also it seems here that these species are so far separated morphologically that kyesamechania exists, although the shape of the copulatory organs is similar. Moreover, wherever *C. bartoni* comes into contact with the burrowing species it generally occupies situations slightly different from those preferred by the chimney-builders. It favors running water in open streams, while the burrowers are found in holes at a certain distance from the streams. Nevertheless, *C. bartoni* is sometimes found in burrows and in springs close to the one or the other of the burrowers (it is even found in the holes of the latter, see p. 414), but in such cases we have again the same conditions as above : different species coming from different centers occupy the same locality.

Yet as a rule *C. bartoni* occupies a different habitat from the burrowers, even if found close to the latter. A fine illustration of this is in Nine-Mile Run, near Pittsburgh. Here three species, *C. bartoni*, *C. monongalensis*, and *C. diogenes* are found together upon a space hardly more than twenty feet square. The locality is a pile of talus swept down into the valley of Nine-Mile Run by a small stream. The stream comes through an insignificant ravine, and spreads out over the talus, forming a kind of a delta, rendering the lower parts of the pile of talus rather

swampy. At the upper end of the talus, in the outcrop of sandstone rock, and not far (about fifteen feet) from the bed of the spring, is a copious spring, the water of which runs directly into the clay and humus of the pile of talus, in a large part underground. *C. bartoni* is found in the small stream under stones; *C. monongalensis* is found at and immediately below the spring referred to; and *C. diogenes* is abundant all over the pile of talus down to the bottom of the valley. At the upper end of the pile of talus is the place where all three species come close together, but each is subject to different ecological conditions.

Similar conditions have been frequently observed, and we thus have here the occupation of the same localities by closely allied species, which differ ecologically, that is to say, *topographical* isolation is not observed here, but the isolation is *ecological*, and the differentiation of the chimney-builders from *C. bartoni* very likely is connected with and largely due to the latter.

(d) C. carolinus and C. monongalensis.

We have seen that these two species are very closely allied, but that the distinguishing characters are constant. Ecologically they are similar, so that hybridisation might occur when they come together. The latter case, however, has never been observed, at least in Pennsylvania, Maryland, and northern West Virginia. The western escarpment of the Chestnut Ridge forms a sharp boundary between them. This case corresponds to that observed in the western river-species (propinquus-group). Two species identical in their ecological habits are separated topographically. But in this case the barrier separating them is of a different character. What the essential feature of this barrier is, is hard to say. Chestnut Ridge in many respects forms a boundary. Altitude seems to play a part, but whether it is paramount is doubtful. Absence of extensive deposits of clay on the western side of this ridge on account of the destruction of the Old Tertiary base-level by subsequent erosion, may also be of importance. Further studies in West Virginia surely will lead to a solution of the question, but this much is certain, that these two species again illustrate the rule that "closely allied species occupy neighboring areas," and further they illustrate the fact that specific differentiation is due to isolation, which is topographical in this case.

What are the actual causes of the difference of the specific characters (color, shape of rostrum, and sculpture of chelipeds), that is to say, what external influences are responsible for them is even more obscure, as it is in the case of the *propinquus*-group.

(e) C. diogenes.

C. diogenes is sharply separated from the other chimney-builders, but resembles them ecologically to a certain degree. In Pennsylvania it comes into contact with them, but in the case of *C. carolinus* this has been observed only once, while it is more frequent in the case of *C. monongalensis*. However, intermediate forms have never been observed, so that we must assume that kyesamechania prevents crossing.

In both cases, with reference to *C. carolinus* as well as *C. monongalensis*, it is to be remarked that whenever one of these is found associated with *C. diogenes* it is always only a contact, not a real mixing of both forms. This is best observed in the case of *C. monongalensis* and *C. diogenes*. All over the range of *C. monongalensis* in southwestern Pennsylvania *C. diogenes*. All over the range of *C. monongalensis* in southwestern Pennsylvania *C. diogenes* is also found. But as has been stated (p. 417 and 458), although they frequently dwell at the same localities they do not occupy the identical locations, *C. diogenes* belonging to a lower level than *C. monongalensis*. Thus we see again a separation, which is primarily expressed in the difference of altitude. Whether the latter is most important seems doubtful. It has been stated that *C. monongalensis* prefers spring-water, while *C. diogenes* lives mostly in swamps, where the water is more or less stagnant and not so cool in summer. (Compare the instance from Nine-Mile Run given above.) But, whatever may be the essential feature which separates both species, it is clear that it is an ecological factor, and, when these two species are found together, it is at a place where the ecological conditions favorable to them come together.

That *C. diogenes* depends on different ecological laws from *C. monongalensis* is also evident from the fact that the former has, outside of Pennsylvania, an entirely different range.

Thus we have here a case similar to that of *C. bartoni* when it associates with the burrowing forms. Two allied species occupy (in Pennsylvania) almost the same territory, and are not separated topographically, but their ecological separation is evident, and very likely is connected with their specific differentiation.

In the two races C diogenes, the eastern and western, we again see the influence of separation. According to our theory that the area of C diogenes was a unit in Preglacial times, and that it was separated by the advancing ice into an eastern and a western section, which subsequently remained separate, we must expect, if isolation effects specific differentiation, that the eastern and western form of C diogenes should show at least a tendency to develop differential characters of specific value. This is indeed the case, as we have seen above (p. 401 et seq).

Isolation, or Habitudinal Segregation, as the factor forming species, is thus clearly seen in every case discussed. We may condense the results obtained in the following sentences.

1. The normal case is when two closely allied species, possessing identical or nearly identical ecological habits occupy separated areas, which lie close together but do not overlap. (Examples : *propinguus*-group ; *C. carolinus* and *C. monongalensis*.)

2. Whenever allied species are found in one and the same locality (overlapping), isolation becomes apparent in the following forms.

(a) The two species have different centers of origin, that is to say, they were separated formerly, but occupied the same territory subsequently. In this case, if very closely allied, hybridization may be possible (*C. obscurus* and *C. sanborni* at New Martinsville, and *C. obscurus* and *C. propinquus* in the Lake Erie drainage), if no kyesamechania exists. If the latter is present, which always means that the two species in question are less closely allied, the two species may actually live side by side under identical conditions (*C. bartoni* and the river-species), or one may conquer and suppress the other. No instances of the latter kind are known in Pennsylvania, but may possibly occur in southwestern Ohio and in Indiana, between *C. rusticus* and *C. propinquus*.

(b) If the centers of origin are more or less identical (absolute identity is hardly possible), the two species always differ ecologically, and although living at the same localities, prefer different surroundings. In this case they are not so closely associated, and they generally remain at a certain distance from one another, although their general areas are overlapping. Under such conditions hybridisation might occur, but it has not been observed in Pennsylvania, and the species existing under such conditions are probably separated by kyesamechania. (Example: C. diogenes and monongalensis.)

Case (a) and (b) may be combined, that is to say, two species living together may have different centers of origin and may be ecologically different. This is seen in the example of *C. bartoni* and the burrowing species.

I believe that in every case where closely allied species overlap in parts of their ranges a close investigation will reveal that one or the other of the above cases is realized. Isolation is, in my opinion, a necessary factor in the differentiation of species, and I do not think that a case ever will be discovered where two closely allied species possess precisely the same distribution. But in order to ascertain this a mere superficial knowledge of the species in question and their range is insufficient, and every case should be investigated as exactly as possible, in a manner similar to the above studies.

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EXPLANATION OF PLATES.

PLATE A.

- FIG. 1. Cambarus obscurus Hageu. Male of the first form, natural size. Collected by the writer, Sept. 7, 1905, in the Alleghany River, Sandy Creek, Allegheny County.
- FIG. 2. Cambarus obscurus Hagen. Fcmale, natural size. From same locality.
- FIG. 3. Cambarus diogenes Girard. Male of the first form, natural size. Collected by the writer, Aug. 26, 1905, at Baden, Beaver County.
- FIG. 4. Cambarus carolinus Erichson. Female, natural size. Collected by the writer, Sept. 5, 1905, at Rainier Park, Ohiopyle, Fayette County.

PLATE B.

- FIG. 1. Cambarus bartoni (Fabricius). Male of first form, natural size. Collected by the writer, Aug. 7, 1905, in Fern Hollow, Pittsburgh.
- FIG. 2. Cambarus bartoni robustus (Girard). Female, natural size. Collected by Miss G. Kinzer, Aug. 27, 1905, at Sixteen Mile Creek, Northeast, Erie County.
- FIG. 3. Cambarus limosus (Rafinesque). Female, natural size. Collected by the writer, Sept. 10, 1905, in the Schuylkill Canal, Manayunk, Philadelphia County.
- FIG. 4. Cambarus monongalensis Ortmann. Female, natural size. Collected by the writer, Aug. 18, 1905, at Edgewood Park, Allegheny County.

PLATE XXXIX.

- FIG. 1. Cambarus bartoni (Fabricius). Rostrum. All figures 4.
 - 1a. Female, 70 mm. long. Collected by the writer, June 3, 1904, in North Versailles Township, Allegheny County, opposite Stewart. Catalogue number 74.327. Shape very broad, margins parallel. Not rare in western Pennsylvania.
 - 1b. Female, 52 mm. long. Collected by the writer, Aug. 22, 1905, at Squaw Run, Allegheny County. Catalogue number 74.626. Shape typical; very frequent.
 - 1c. Male, first form, 63 mm. long. Collected by the writer, Sept. 16, 1904, at Valley Forge, Chester County. Catalogue number 74.413. Shape typical, and characteristic of eastern specimens, but also found in the west.
 - 1d. Young male, second form, 34 mm. long. Collected by the writer, Aug. 22, 1905, in Squaw Run, Allegheny County. Catalogue number 74.626. Usual shape in young specimens.
 - Young female, 21 mm. long. Collected by the writer, June 25, 1904, in Jacob's Creek, Laurelville, Fayette County. Catalogue number 74.356. Slightly longer than usual, but not rare in young specimens.
 - 1f. Male, first form, 78 mm. long. Collected by the writer, May 27, 1904, in Squaw Run, Allegheny County. Catalogue number 74.320. Unusually short and strongly tapering, with exceptionally thick margin.

- FIG. 2. Cambarus bartoni robustus (Girard). Rostrum. 4.
 - 2a. Female, 89 mm. long. Collected by the writer Oct. 4, 1904, in Temple Creek, Albion, Erie County. Catalogue number 74.435. Normal shape.
 - 2b. Young female, 18 mm. long. Collected by Miss G. Kinzer, Aug. 27, 1905, in Sixteen-Mile Creek, Northeast, Erie County. Catalogue number 74.630. Normal shape in young specimens.
- FIG. 3. Cambarus carolinus Eriehson, Rostrum. 4.
 - 3a. Male, first form, 66 mm. long. Collected by the writer, Sept. 5, 1905, at Ohiopyle, Fayette County. Catalogue number 74.640. Normal shape.
 - 3b. Male, seeond form, 30 mm. long. Collected by the writer, June 11, 1904, at Indian Creek, Fayette County. Catalogue number 74.365. Shape exceptional. Most extreme case as regards convergence of margins.
- FIG. 4. Cambarus monongalensis Ortman. Rostrum. 4/1.
 - 4a. Male, first form, 63.5 mm. long. (Type.) Collected by the writer, May 21, 1905, a
 Edgewood Park, Allegheny County. Catalogue number 74.316. Normal shape.
 - 4b. Female, 73 mm. long. Collected by the writer, Oct. 12, 1904, at Hill, Westmoreland County. Catalogue number, 74.449. Shape unusually broad, and margins almost parallel. Most extreme ease in this direction, standing rather isolated.
- FIG. 5. Cambarus limosus (Rafinesque). Left first pleopod of male, first form. 3.
 - 5a. Inner view. Collected by the writer, Sept. 19, 1904, in Marcus Hook Creek, Mareus Hook, Delaware County. Catalogue number 74.423.
 - 5b. Posterior view of same.
- FIG. 6. Cambarus propinquus Girard. Left first pleopod of male. ³/₁.
 - 6. Inner view, male, first form. Collected by the writer, Oct. 4, 1904, in Temple Creek, Albion, Erie County. Catalogue number 74.439.
 - 6b. Inner view, male, seeond form. Collected by the writer, June 7, 1904, in a tributary of Conneaut Creek, Conneautville Station, Crawford County. Catalogue number 74.336.
- FIG. 7. Cambarus obscurus Hagen. Left first pleopod of male. $\frac{3}{1}$.
 - 7a. Inner view, male, first form. Collected by the writer, Aug. 24, 1904, in the Ohio River, Ambridge, Beaver County. Catalogue number 74.401.
 - 7b. Posterior view of same (horny tip of outer part hidden behind inner part).
 - 7c. Inner view, male, second form. Collected by the writer, June 24, 1904, in the Loyalhanna River, Crisp, Westmoreland County. Catalogue number 74.352.
 - 7d. Inner view, hermaphroditie specimen (type of male, first form). Collected by Atkinson, Graf, and Williamson, May 14, 1899, in the Ohio River, Neville Island, Allegheny County. Catalogue number 7.436. (See text, p. 376.)
 - 7e. Posterior view of same.

- FIG. 8. Cambarus bartoni (Fabricius). Inner view of left first pleopod of male, first form. $\frac{3}{1}$. Collected by the writer, Oct. 6, 1905, at Weskit, near Kittanning, Armstrong County. Catalogue number 74.665.
- FIG. 9. Cambarus carolinus Erichson. Inner view of left first pleopod of male, first form. ³/₁. Collected by the writer, Sept. 7, 1904, at Dunbar, Fayette County. Catalogue number 74.410.
- FIG. 10. Cambarus monongalensis Ortmann. Inner view of left first pleopod of male, first form (cotype), ³/₁. Collected by the writer, Oct. 10, 1903, at Edgewood Park, Allegheny Connty. Catalogue number 74.182.
- FIG. 11. Cambarus diogenes Girard. Inner view of left first pleopod of male, first form. $\frac{3}{1}$. Collected by the writer, September 5, 1904, at Smithfield, Fayette County. Catalogne nnmber 74.406.

PLATE XL.

- FIG. 1. Cambarus obscurus Hagen. Upper view of right chela of a male, first form, 77 mm. long, natural size. Collected by the writer, Sept. 30, 1905, in the Alleghany River, Twelve-Mile Island, Allegheny County. Catalogue nnmber 74.663.
- FIG. 2. Cambarus bartoni (Fabricins). Upper view of right chela of a male, first form, 82 mm. long, natural size. Collected by the writer, Nov. 22, 1905, in Fern Hollow, Pittsburgh, Allegheny Connty. Catalogue number 74.681.
- FIG. 3. Cambarus bartoni robustus (Girard). Upper view of right chela of a male, first form 98 mm. long, natural size. Collected by the writer, July 11, 1905, at Spartansburg Crawford County. Catalogne nnmber 74.596.
- FIG. 4. Cambarus carolinus Erichson. Upper view of right chela of a female, 77 mm. long, natural size. Collected by the writer, Oct. 16, 1905, at Dunbar, Fayette County. Catalogue number 74.669.
- FIG. 5. Cambarus monongalensis Ortmann. Upper view of right chela of female, 71 mm. long, natural size. Collected by the writer at Edgewood Park, Allegheny County, April 4, 1905. Catalogne number 74.495.
- FIG. 6. Cambarus diogenes Girard. (Eastern form.) Upper view of right chela of a male, first form, 83 mm. long, natural size. Collected by the writer, Sept. 21, 1905, at Ridley Park, Delaware County. Catalogue number 74.654.
- FIG. 7. Cambarus diogenes Girard. (Western form.) Upper view of right chela of a male, second form, 93 mm. long, natural size. Collected by the writer, April 15, 1905, at Millvalle, Allegheny County. Catalogue number 74.507.
- FIG. 8. Burrow of Cambarus bartoni (Fabricius). In spring on hillside, west of Spruce Run, Avalon, Allegheny County, opened by the writer, July 2, 1904.
 - 8a. Side view (section); 8b. Upper view. mp, pile of mud consisting of clay, sand, and small stones; d, ditch; x, place where crawfish, female, 52 mm. long, was found. At x springwater was running into the hole in a strong flow, and running out through the hole, over and past the pile of mud into a ditch.

- FIG. 9. Burrow of *Cambarus carolinus* Eriehson, located in a swampy place in stiff yellow elay, at Listie, Somerset County. Opened by the writer Aug. 12, 1904.
 - 9a. Diagram of disposition of piles of mud seen from above. 9b. Section of hole along line A-D. 9c. Section of hole along line A-B-C. A. Open ehimney. B. Closed ehimney. D. Closed ehimney, hole filled up a good distance below surface of ground. C. Open hole, without pile of mud, situated under the edge of a large flat stone (s). wl, water level; x, place where the erawfish (male, first form, 61 mm. long) was found.

Plate XLI.

- FIG. 1. Burrow of *Cambarus bartoni* (Fabrieius). Located in the sand and gravel of the dry bed of a small stream, Edgewood Park, Allegheny County. Opened by the writer, Oct. 10, 1903. *mp*, pile of mud, eonsisting of mud, sand, and gravel; *s*, large slab of stone, lying imbedded in sand and gravel; *wl*, water level (the stream was dry for long stretches, only here and there pools of water were left); *x*, place where erawfish (female, 63.5 mm. long) was taken.
- FIG. 2. Burrow of Cambarus monongalensis Ortmann. Located in yellow elay (mixed with humus), at a springy place on the bank of small stream, near Monongahela City, Washington County. Dug out by the writer, June 16, 1904.
 - 2a. Diagram of burrow and chimneys, seen from above; 2b, section of hole along line A-B-C; 2c, section of hole along line C-D-E. A, hole opening laterally, with one-sided pile of mud in front, keeping up the level of water; B and D, elosed chimneys; C, open, large, and regular chimney; wl, water level; st, stream; x, places where the old female (mother, 65 mm. long), and ten young (20.5 to 32.5 mm. long) were found. Water, in a weak flow, was running in at E, and was running out at A.
- FIG. 3. Burrow of *Cambarus monongalensis* Ortmann. Loeated in yellow elay, at a springy place on the bank of a small stream, Edgewood Park, Allegheny County. Dug out by the writer, May 9, 1904. The burrow is of a type similar to the one figured in Fig. 2, but less eomplex. *a*, hole opening laterally, with one-sided pile of mud keeping up the level of the water ; *b*, elosed ehimney ; *wl*, water level ; *st*, stream ; *x*, place where the erawfish (female, 63 mm. long) was taken.
- FIG. 4. Burrow of Cambarus monongalensis Ortmann. Located in black muck, at a springy and swampy place at the bottom of the upper part of Fern Hollow, Pittsburgh, Allegheny County, opened by the writer, Oct. 18, 1903. Type of a hole in level ground, with the water near the surface. No adults and only four young were found in this hole, but possibly the hole had additional branches, which were not discovered, the high stage of the water and its iey coldness rendering investigation difficult. About 1.50 m. from this hole another was opened, which contained a female C. diogenes. a, elosed chimney ; b, one-sided chimney in front of hole opening obliquely ; wl, water level ; x, places where young specimens (11.5 to 16.5 mm. long) were found.

- FIG. 5. Burrow of Cambarus diogenes Girard. Located in stiff blue clay, in a ditch on a road-side, Nine-Mile Run, Pittsburgh, Allegheny County. Opened by the writer, Nov. 5, 1904. The season had been very dry, and not much water was in the hole. Pebbles were lying on the bottom of the hole. a, old chimney, leveled down by rain, probably built in spring; b, fresh mud, brought up recently (beginning of fall activity); wl, water level; x, place where the specimen (female, 77 mm. long) was taken.
- FIG. 6. Burrow of Cambarus diogenes Girard. Located in yellow clay and humus, at a springy and swampy place in woods on the side of a wagon road, upon which water was standing (after a heavy thunder-shower on the previous day), at Squaw Run, Allegheny County. Dug out by the writer, May 27, 1904. a, chimney, consisting of yellow clay; b, "stopper" in the mouth of the chimney, distinctly differing from the chimney, the material being yellow clay mixed with blackish mud and leaf-mould; wl, water level; r, road, with mud-puddle upon it; x, place where the crawfish (male, first form, 76 mm. long) was found.
- FIG. 7. Burrow of *Cambarus diogenes* Girard. Located in yellow and blue clay, on the border of a swampy place, Schenley Farm, Pittsburgh, Allegheny County. After a sketch furnished by Mr. F. E. Kelly, Nov. 14, 1904. *sw*, swamp; *bc*, blue clay; *yc*, yellow clay; *a*, one-sided chimney, consisting of yellow clay (probably made in spring and summer); *b*, new chimney, consisting of blue clay (fall activity, reclaiming of old burrow at *c*); *c*, old burrow, filled in (during summer) with blue clay, taken or washed in from near the mouth of the lower entrance (*a*) of burrow; *wl*, water level; *x*, place where the crawfish was taken.
- FIG. 8. Burrow of Cambarus diogenes Girard. Located in blue and yellow clay on the bank of a small stream, Schenley Farm, Pittsburg, Allegheny County. After a sketch drawn by Mr. F. E. Kelly, Nov. 15, 1904. s, stream; bc, blue clay; yc, yellow clay; a, new chimney, consisting of yellow clay, evidently coming from the newly dug shaft going down vertically; b, upper end of ascending branch of hole, without opening (possibly originally open, but sealed up, and the pile of mud overgrown and obliterated by vegetation); wl, water level; x, place where the crawfish was taken. The chimney at a shows fall activity, and the vertical shaft is being built by the

crawfish in order to get deeper down into the ground.

PLATE XLII.

- FIG. 1. Preglacial Monongahela River, after Leverett (1902, p. 89, fig. 1).
- FIG. 2. Present range of *Cambarus obscurus* Hagen and *C. propinquus* Girard. (Including variety sanborni (Faxon)).
- FIG. 3. Distribution of Cambarus propinquus Girard, propinquus sanborni (Faxon), and C. obscurus Hagen.

(For further explanation, see legend on map, and text, p. 433-446).
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PLATE XLIII.

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Map of Pennsylvania, showing distributional areas of crawfishes. (See Legend on map, and text, p. 465-466).

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PLATE A



FIG LZ AMBAPUS BECURUS HAGEN. CAMBARUS DUJGENES GIRARD. 4 CAMPAPUS CAROLINUS ERICHECH





FIC LAMBARUS LIMUEUS RAFINESI, JE-1 ZEESEWINGHIGH CO. H. Y. FIC. 4. CAMBAPUS MONONGALENSIS ORTMANN

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PLATE XXXIX.



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MORPHOLOGICAL DETAILS OF GENUS Cambarus.

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Memoirs Carnegie Museum, Vol., II.

PLATE XL.



CHELE OF Cambarus, FIGS. 1-7. BURROWS OF Cambarus, FIGS. 8-9.

MEMOIRS CARNEGIE MUSEUM, VOL. II.

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PLATE XLI.



BURROWS OF Cambarus.





